University of Sassari
Ph.D. School in Natural Sciences
Via Muroni 25, I-07100 Sassari, Italy

Dissertation for the Degree of Doctor of Philosophy in Environmental Biology
presented at Sassari University in 2014

XXV cycle

NORTHERN- AND SOUTHERN EUROPEAN GREY WOLF *(Canis lupus)* PREY CHOICE, ROLE AS THE KEYSTONE SPECIES IN A SCAVENGER COMMUNITY AND ACTIVITY PATTERN

PH.D. CANDIDATE: ***Sophie Ståhlberg***

DIRECTOR OF THE SCHOOL: ***Prof. Marco Curini Galletti***

SUPERVISOR: ***Prof. Marco Apollonio***

University of Sassari
Ph.D. School in Natural Sciences
Via Muroni 25, I-07100 Sassari, Italy

Dissertation for the Degree of Doctor of Philosophy in Environmental Biology
presented at Sassari University in 2014

XXV cycle

NORTHERN- AND SOUTHERN EUROPEAN GREY WOLF *(Canis lupus)* PREY CHOICE, ROLE AS THE KEYSTONE SPECIES IN A SCAVENGER COMMUNITY AND ACTIVITY PATTERN

PH.D. CANDIDATE: ***Sophie Ståhlberg***

DIRECTOR OF THE SCHOOL: ***Prof. Marco Curini Galletti***

SUPERVISOR: ***Prof. Marco Apollonio***

SUMMARY

[ENGLISH] Grey wolf is an elusive, widely but sparsely distributed and difficult to observe predator, highly adaptable and capable of adjusting to different ecological conditions. I studied the prey choice of wolf in Scandinavia and Tuscany and looked at variances between territories within the two study areas. I analysed scats collected during a nine year period in Scandinavia and four years in Tuscany. I found greater habitat heterogeneity in Tuscany which leads to a more complex predator-prey structure while in Scandinavia, the seasonal prey type choice was more dynamic. Reasons may be related to the fact that there is a highly exploited forestry industry in Sweden disabeling rich ecological diversity. The Tuscan Apennines has the recent decades been depopulated as abandoned agriculture allows re-forestation and ungulate species abundance to increase. I did a movement triggered camera study of the scavenger guild in wolf territories feeding on wolf killed, or death by other causes, carcasses and analysed 24 h and seasonal activity patterns. I also looked at anti-predator behaviour in intra-guild members using these feeding sites. I discovered in both the diet study and the camera study that there was no avian prey in the wolf diet in Tuscany, nor avian scavengers at the carcass sites in the Tuscan Apennines. There is a trade-off between time spent feeding and anti-predator behaviour and I quantified the level of vigilance in scavenger species in the Tuscan Apennines. I then compared safety investment by vigilance behaviour in Tuscan and Swedish scavengers, specifically red fox and marten, and found that martens in the Tuscan Apennines feed more and invests less in anti-predator behaviour than their Swedish conspecifics.

KEY WORDS: *Canis lupus,* prey selection, scat analysis, habitat variation, preditor-prey constitution, movement-triggered camera system, scavenger, intra-guild interaction

RIASSUNTO

[ITALIAN] Il lupo è un predatore elusivo, con un ampio areale di diffusione in cui è distribuito in modo irregolare. Il predatore è estremamente plastico e in grado di adattarsi ad un ampio range di situazioni ecologiche. In questo lavoro ho analizzato la scelta delle prede in Scandinavia ed in Toscana (Italia), ponendo attenzione alle differenze tra i diversi territori all'interno delle aree di studio. Le fatte analizzate per l'analisi della dieta sono state raccolte in un periodo di 9 anni in Scandinavia e 4 anni in Toscana. In Toscana si è riscontrata una maggiore eterogeneità dell'habitat, il che porta ad una maggiore complessità nella struttura del rapporto preda-predatore, mentre in Scandinavia è presente una maggiore dinamica stagionale nella scelta delle prede. Le ragioni di questo potrebbero essere legate alla massiva diffusione dell'industria forestale in Svezia, che riduce la diversità ecologica. Nelle ultime decadi l'Appennino Toscano ha subito un processo di spopolamento, che ha portato alla riforestazione di ampie aree, favorendo un aumento numerico delle popolazioni di ungulati.

Inoltre abbiamo studiato il comportamento degli necrofagi nell'area di studio. Questo studio è stato svolto cercando nel territorio le carcasse degli animali o uccisi dal lupo o morti per altre cause, e una volta rinvenuta la carcassa, posizionando delle foto trappole. Questo non solo ci ha permesso di studiare i ritmi di attività giornalieri e stagionali delle specie che hanno visitato le carcasse, ma anche di analizzare il comportamento antipredatorio delle diverse specie ai siti con le carcasse, misurando il tempo di vigilanza di ogni specie. Dall'analisi degli escrementi e dei video si è osservato che nella dieta del lupo non sono presenti specie di uccelli e che in Toscana questi ultimi non sono presenti tra le specie che utilizzano le carcasse. Per le diverse specie inoltre esiste un compromesso tra il tempo speso per alimentarsi ed il comportamento antipredatorio. Infine Ho comparato il tempo di vigilanza alle carcasse speso da volpe e martora in Svezia e Toscana; la martora in Toscana investe meno tempo nella vigilanza.

PAROLE CHIAVE: *Canis lupus,* selezione delle prede, analisi degli escrementi, variazioni dell'habitat, sistema preda-predatore, fototrappole con sensori di movimento, necrofagi, interazioni intra-associazioni

List of publications

My thesis is based on the work contained in the following papers, referred to by Roman numerals in the text:

I – Wikenros, C., Ståhlberg, S., Sand, H. 2013. Feeding under the risk of intraguild predation: vigilance patterns of two medium sized generalist carnivores. *Journal of Mammalogy*

II – Ståhlberg, S., Bassi, E., Viviani, V., Apollonio, M. 2013. Quantifying prey selection of northern and southern European wolves *(Canis lupus):* Scandinavia and Tuscany.

III – Ståhlberg, S and Apollonio, M. 2013. Scavenger temporal and spatial selection of visits at feeding sites in north and south European wolf territories.

IV – Ståhlberg, S. and Apollonio, M. 2013. The function of vigilance in sympatric facultative scavengers in an Apennine wolf territory.

1 INTRODUCTION

1.1 Intraguild predation and andti-predator behaviour - Paper I and IV

Predation by top predators on intermediate predators may not only reduce competition through a numerical effect on the intermediate predators, but should also lead to a change in behaviour with an increased vigilance of the targeted species (Kimbrell et al 2007). A successful strategy maximises feeding rate while minimising the risk of predation and in some mammals, habitat shifts result in reduced foraging opportunities (Sih 1980; Lima & Dill 1990). Predators should concentrate their search effort on those patches yielding greatest net gain of energy, although other factors, such as nutrient constraints and predation risk, may also influence the foraging decisions (Tinbergen 1981) and large carnivores play an important role maintaining balance in all trophic levels in terrestrial ecosystems (Hebblewhite et al 2005; Beschta & Ripple 2009). Several approaches, from direct lethal predation to indirect behavioural effects that alter prey distribution and habitat selection by intraguild members and prey species, are utilised by top predators (Lima & Dill 1990; Berger et al 2008; Kittle et al 2008).

Keystone species, such as the grey wolf, are however not only a predation risk for intermediate predators, they also abandon incompletely consumed carcasses for scavenging species. As top predators are not as dependent on winter carrion and thereby not as attracted to carcass sites, other mesopredators such as red fox, may have less interference competition with wolves and higher presence at carcass sites (Linell & Strand 2000). The behavioural response of a prey or subdominant species to

temporarily varying predation risks emphasises the behavioural plasticity of this species (Griffin et al 2002; Sönnichsen et al 2013).

1.2 Wolf feeding ecology - Paper II

An animal exhibits a preference for a particular type of food when the proportion of that type in the animal's diet is higher than its proportion in the environment (MacArthur and Pianka 1966). Ranked preferences are usually seen most clearly amongst carnivores who actively select prey items that are the most profitable in terms of energy intake per unit time spent handling prey, i.e. the "functional response", classified by Holling (1959*a,b*). Wolves are highly adaptive and behaviourally flexible carnivores that have evolved to hunt prey widely ranging in size, although they are most commonly categorised as cursorily hunters of large ungulates (Peterson and Ciucci 2003).

Wolves are most often territorial and hunt within their home range where the prey species are determined by the habitat resources and threats. When wild prey species are limited or scarce, they are opportunistic and have the ability to utilise other food sources such as domestic animals, garbage, carcasses, marine species and vegetation (Salvador and Abad 1987; Okarma 1995; Darimont et al 2003; Stahler et al 2006; Watts et al 2010). Moreover wolves can both scavenge and predate, and they switch between the two strategies depending on what is most profitable (Stephens & Krebs 1986). Furthermore, it is obvious that when the environmental characteristics change, the relation between wolves and preys changes as well. During the past decades, many studies have been carried out to define wolves food habits in different areas, and one common result is that ungulates are the main preys within its range (Sand et al 2005; Meriggi et al 2011); moreover nearly all ungulates species are used by wolves within their range, and it seems that in each local area wolf became very skilled on hunting a specific one (Sand et al 2012). Extensive information regarding the feeding ecology of wolves using scat analysis have been done in Italy (Mattioli et al 1995 and 2011; Capitani et al 2004; Gazzola et al 2007; Meriggi et al 2011; Milanesi et al 2012) but very few in Scandinavia. Paper II describes wolf prey selection in northern and southern Europe, using scat analysis.

1.3 Scavenger tempo-spatial partitioning - Paper III

Scavengers play an essential role in terrestrial ecosystems by accelerating the return of nutrients to trophic webs, distributing such nutrients over a wide area, and reducing potentially infective foci (DeVault et al 2003). In many ecosystems, it is likely that more energy is transferred through scavenging of carrion than through predation of live animals (Wilson and Wolkovich 2011), reflecting a major underestimation of the importance of carrion as a resource to vertebrate communities. The mortality factor of animal carcasses vary widely depending on different ecosystems abiotic factors; climate, soil, nutrient cycling, regeneration, forest fires and landslides, as well as biotic factors; herbivory, presence or absence of effective predators, human activity, disease and insect outbreaks (Houston 1979;

Bergerud 1980; Frelich 2002; DeVault et al 2003). Scavengers, microbes, fungi and arthropods compete for cadaveric resources and the time of detection of the carcass is crucial. In cold climate regions or seasons when microbes, fungi and arthropods are less active, vertebrate scavengers monopolise the nutritional food source of carcasses (Putman 1983).

Common vertebrate scavengers are birds with excellent visual capability and availability of scanning large areas but mammals have the advantage in e.g. forested areas with limited visibility or dark hours when birds are inactive. Scavenging species may choose several food recourses with temporal-, spatial- and cost dependant variances, carrion being most available in late winter when many herbivore species suffer from food shortage, weakness and starvation. The use of carrion as a supplemental food resource during prey shortages may have substantial impacts on the population dynamics of predators and their prey (DeVault et al 2003). Carrion consumption may expose potential scavengers to risks such as disease (Jenelle et al 2009), conflicts with other scavengers (May et al 2008) and exposure to predation (Merkle et al 2009), yet the benefits of scavenging over predation may offset these risks.

Large and medium sized scavenging species may be outcompeted by smaller sized though numerical superiority or aggregations, nonetheless, increments in carrion availability may allow scavenging species to reach higher densities by compressing home range sizes (Blàzquez et al 2009). Larger predators do kill intermediate predators when interfering at carcass sites (Lindström et al 1995; Berger & Gese 2007), however, smaller species may take advantage of larger predators by following or adjusting their behaviour temporarily or spatially (Macdonald et al 2004; Atwood & Gese 2010; Mattisson et al 2011). Small carcasses are usually consumed rapidly by scavengers (Travaini et al 1998; DeVault et al 2004), while in the temperate regions of the northern hemisphere, large carcasses may last several months (Green et al 1997).

Whereas carcasses produced from natural mortality is seasonally pulsed, wolf-killed prey species provide a more constant and predictable food resource for scavengers over the year (Wilmers et al. 2003; Selva & Fortuna 2007). In Yellowstone, wolf restoration has resulted in important changes on the ecosystem by altering the quantity and timing of carrion available to scavengers (Wilmers et al 2003). Contrary to live prey, carcasses represent a food resource that may trigger inter- and intraspecific conflicts during feeding bouts at feeding sites. Thus, temporal and spatial segregation among species and individuals are necessary to avoid intraguild predation and conflict. As seen in previous studies (Wikenros et al 2013), temporal partitioning of the usage of food resources can be in a fine scale with only a few hours or minutes of differentiation. Paper III compares northern and southern European scavenging guilds in wolf territories using movement triggered camera systems.

2 OBJECTIVES

The aim of my thesis is to investigate prey selection in northern and southern European wolves and identify ecological factors affecting their feeding behaviour beyond latitude, prey species and human density. As a keystone species and top predator in an ecosystem, grey wolf affects other trophic levels by regulation of herbivory, predation, food supply and competition with other predators and humans. Remains after wolf kills are an additional food source for scavenging species and I used motion triggered camera systems in south-central Sweden and the Tuscan Apennines for monitoring intra-guild interactions. Exact time of scavenger as well as wolf activity, 24 h and seasonal activity patterns were recorded. My questions in the papers were;

Paper I – What is the level of vigilance in two medium sized generalist species, pine marten *(Martes martes)* and red fox *(Vulpes vulpes)* scavenging at a wolf-killed carcass? Does predator size affect the pattern of predator scavenging and behaviour?

Paper II – Are prey species with the highest density selected by wolves? Does size difference in Italian and Swedish wolves affect prey selection? Does Scandinavian wolves select juvenile moose more than Tuscan wolves selects cervid fawns due to the predator-prey size relation? Does the higher human density in Italy result in a higher proportion of domestic animals in the diet than in Scandinavia?

Paper III – What are similarities and dissimilarities in scavenging species utilising feeding sites in wolf territories in south-central Sweden and the Tuscan Apennines and what are the daily and seasonal activity patterns? Is the wolf a common scavenger in these two areas?

Paper IV – Are there intra-guild predation or interactions in the scavenger guild at carcasses/feeding sites in the Tuscan Apennines, Alpe di Catenaia? Which are important factors affecting the level of vigilance? Does larger body sized scavengers follow smaller? Does the lack of avian predators result in less vigilance?

3 STUDY AREAS

3.1 General description

South-central Scandinavia

20 study territories in south-central Scandinavia, mainly in Sweden in the counties Värmland, Dalarna, Örebro, Västra Götaland and two in Norway. Boreal temperate forests in the cold temperate climate zone with snow cover 3-6 months/year. Coniferous forest is the dominant vegetation type and the climate is continental with temperatures ranging from 15°C in July and –7°C in January,

precipitation 600-1200 mm/year. Scandinavia's boreal forests (300 000 km^2 in Norway and Sweden) are among the most intensively exploited forests in the world, with less than 5% virgin forest left standing. Naturally reseeded or replanted stands are clear-cut on a 70–80 year cycle using a highly mechanised system and a dense network of forest roads (Linnell et al 2000). The vegetation is dominated by coniferous forests of Scots pine *(Pinus sylvestris)* and Norway spruce *(Picea abies)*. Common deciduous species included birch *(Betula pubescens)*, willow (Salix spp), aspen (*Populus tremula*), and alder (*Alnus incana, A. glutinosa*). Human population density in Sweden 20/km^2, but in the study area the density is less than 1/km^2 (Swedish National Atlas 1991). Due to extensive logging, the study areas are easily accessible to humans by a network of gravel forest roads (0.62 km/km^2) (Eriksen et al 2009). Human hunting for wild ungulates is a very widespread, but carefully regulated, activity (Cederlund and Bergström 1996).

The three study areas in *Tuscany, Italy*, are two in the Tuscan Apennines; *Alpe di Catenaia*, 490-1400 m.a.s.l. - Arezzo province, *Orecchiella*, 900-2054 m.a.s.l. - Lucca province, and one in the transition zone between the mountains and the Mediterranean coast, *Val di Cecina (Berignone)* – Pisa province. The Tuscan Apennines has a continental climate characterised by high humidity with mean temperature summer 17.5° C and winter 8° C. Precipitation 1000-1600 mm/year. High forest cover with a frequency of coppice mixed with pine and black pine *(Pinus negra)*, white spruce *(Picea glausa)*, Douglas fir *(Pseudotsuga spp)*, birch *(Betula spp),* ash *(Fraxinus excelsior)* and lower bands of Turkey oak *(Quercus cerris)* and chestnut *(Castanea spp)*. *Berignone,* 100-600 m.a.s.l., close to the Tyrrhenian coast. Mean temperature between 9 and 18 ° C and precipitation 300-1500 mm/year. Wooded hills composed of deciduous and evergreen oak forests of *Quercus pubescence, Q. robur* and *Q. ilex*. Human density: 107/km^2, 210/km^2 and 161/km^2 in Arezzo, Lucca and Pisa province but the actual inhabitants inside the study areas are <0,5/ km^2. Mean road densities inside the study areas are <1.5 km/km^2. The three study areas can be included in an area of about 8 000 km^2.

3.2 Wolf populations

South-central Sweden

Intensive persecution of wolf during the nineteenth and twentieth century exterminated these predators from most of the Scandinavian peninsula by the mid-to-late 1800s (Wabakken et al 2001), and they were functionally extinct from the whole peninsula by late 1960s (Haglund 1968). By the late 1970s, wolves reappeared and there has been successful reproductions all years but 1986 (Wabakken et al 2001). Today, the Scandinavian Peninsula has a recolonizing wolf population of 252-291 individuals (Wabakken et al 2010). Most part of the population is located in south-central Sweden where wolves have been protected since 1966 until 2010 and 2011, when the government introduced licensed hunting which was haltered after

formal complaints to the EU commission regarding violation of the EU Habitat and Species Directive. The Scandinavian population has a high inbreeding coefficient (Liberg et al 2005) as it originated from 3 individuals successfully reproducing in 1983 and has natural immigration from the Finish-Russian source population (Linell et al 2005). The predicted need for 1-2 immigrants per generation to prevent loss of genetic diversity is prevented by the reindeer husbandry in the north of Sweden and Finland (Pedersen et al 2003). Other main threats decreasing survival and reproduction success are poaching (Liberg et al 2011) and traffic collisions (Mörner et al 2005).

Tuscany, Italy

The estimated wolf population size in Italy is approximately thousand individuals, even though exact numbers are lacking, it has increased in recent years (Boitani 2003). The expanding population is recolonizing the Alps and indicates that migration has been unidirectional from the Apennines to the Alps, and that wolves in southern Italy did not contribute to the Alpine population. Tuscany is located in North-central Italy and is a probable source of dispersing wolves to the Alps (Scandura et al 2001; Fabbri et al 2007). Wolf habitat status differs between geographical areas and I examined wolf territories in three areas in Tuscany for a more comprehensive overview.

3.3 Prey species

South-central Sweden; most abundant prey species in the territories are moose *(Alces alces)*, with an average population density estimated from pellet counts at 1.1±0.1 moose/km^2 during winter (Sand et al 2005). Other prey species available included roe deer *(Capreolus capreolus)*, (approx. 0.01/ km^2), beaver (*Castor fiber*), mountain hare (*Lepus timidus*), capercaillie (*Tetrao urogallus*), black grouse (*Tetrao tetrix*). Red deer *(Cervus elaphus)*, fallow deer *(Dama dama)* and wild boar *(Sus scrofa)* are present in low numbers in some territories, but had no significant value in the results.

Tuscany; wolves most preferred ungulate prey species in the northern Apennines, wild boar and roe deer, has increased significantly between 1977-2004 (Meriggi et al 2011). In Alpe di Catenaia; wild boar, roe deer fallow deer, red deer. Orecchiella; mouflon *(Ovis orientalis musimon)*, red deer, roe deer, wild boar. In Val de Cecina – Berignone; wild boar, fallow deer, roe deer, mouflon and small mammals are common. Sheep and goats are present in open areas throughout the year.

3.4 Scavenging species

Scavengers in south-central Sweden was the red fox *(Vulpes vulpes)*, common raven *(Corvus corax)*, pine marten *(Martes martes)*, European jay *(Garrulus glandarius)*, common buzzard *(Buteo buteo)*, goshawk *(Accipiter gentilis)*, golden

eagle *(Aquila chrysaetos)*, hooded crow *(Corvux cornix)*, wolf, magpie *(Pica pica)*, badger *(Meles meles)*, brown bear *(Ursus arctos)*, domestic dog *(Canis familiaris)*, wild boar *(Sus scrofa)* and only a few visits by eagle owl *(Bubo bubo)*, sea eagle *(Haliaeetus albicilla)*, wolverine *(Gulo gulo)* and lynx *(Lynx lynx)*. In the Tuscan Apennines, there was red fox followed by pine and stone marten *(Martes foina)*, badger, dog, wolf, wild boar, wildcat *(Felis sylvestris)*, birds of prey, *Corvidae spp* and polecat *(Mustela putorius)*.

4 METHODS

4.1 Scat analysis (Paper II)

In Scandinavia, the scats were frozen and prior to the analyses the scats were dried for 48h at 90°C (±5°C). After the drying process, dry weight of the scats was taken (0.01g precision). The procedure to analyse the scat contents followed Spaulding et al. (1997). Each scat was broken apart by hand and the single prey items were sorted. If there was more than one prey item found in the scat, we assumed that the macro and micro components originated from the found items in the same proportion (Ciucci et al 1996). We identified the macro components in the scats (e.g. bird remains, hairs, hooves, teeth) with the help of reference manuals (Moore et al 1974, Debrot et al 1982, Teerink 1991) and a reference collection developed at the Grimsö Research Station. The hairs were first examined visually concerning colour pattern, length, thickness, and thereafter identified microscopically by medullary pattern and cuticular scale (Teerink 1991). With the help of a reference grid we visually estimated the relative volumetric proportion for each prey item identified in a scat (Reynolds & Aebischer 1991). The distinction into juvenile and adult cervids was carried out due to the characteristic hair pattern of young animals. We were not able to distinguish consistently between juvenile and adult animals because the typical juvenile hair pattern is only visible from birth to the first autumn moult in August/September. Because of that, it is not possible to distinguish between juveniles and adults during the winter season by looking at the hairs (Peterson et al. 1984, Ciucci et al. 1996). To make a reasonable differentiation into juveniles and adults we applied the age class distribution for consumed cervids described by Pedersen et al (2005) according to: moose, adults:yearlings:calf = 80:10:10 and roe deer, fawns:adults = 50:50.

In Italy, the scats were kept dry and frozen at -30°C, scat were washed in a sieve of 0.5 mm and the prey remains (hairs and bones), fruit and grasses found in every scat were dried at 68°C for 24 h. Prey remains were identified through comparison to a reference collection of mammal hair, bones, and teeth. We identified the prey species and age or weight class (for ungulates only) when possible. This identification was based on the macroscopic characteristics of hairs and bones following Mattioli et al. (2004, and 2011). Wild boar remains were divided into three weight classes: newborn piglet (<10 kg), piglet (10–35 kg), and adult (>35

kg). Cervid remains were classified into two classes according to the first moult at 6 months of age: fawn (<7 months) and adult (≥7 months), equivalent to the Scandinavian classification. In order to estimate the contribution of each species in the diet, in terms of volume, we categorized each food item in a scat by 5% steps (i.e. <5%; 6–10%; 11–15%) as described by Russell and Storch (2004). We calculated the average volume (AV%) for each food item. The AV% was defined as $V_i/N \times 100$ where V_i is the total volume of a given food item i, and N is the total number of scats.

4.2 Movement triggered camera systems (Papers I, III and IV)

Movement-triggered cameras were placed at carcasses killed by wolves, remains from hunter harvest or ungulates killed in traffic collisions all year round. Cameras were set up when collared wolves where >2 km away from the carcass. Sites with remains from moose harvest were reported by hunters and cameras were set up the same day as shot. Because many mammals reacted to flash light used, we removed the light and changed to longer wavelength creating invisible infrared light, or replaced them with other brands. Date and time were registered on each photo/film. Cameras were placed on tree stems approximately 0.5-2.5 m above ground, depending on site location and terrain ruggedness (Sappington et al 2005) as well as risk of scavenger interference, 2-10 m from carcasses. The movement detectors were not triggered by birds smaller than jay or mammals smaller than martens. Camera sites were checked and memory cards and/or batteries changed every 1-6 week except for two cameras which used GPRS/MMS transmission and one of these had a solar cell panel as energy source. One feeding bout could consist of a large number of films/photos, why we classified a visiting occasion as per individual with ≥11 min between visits.

4.3 Additional data and processing

Data was kindly obtained from the Swedish National Veterinary Institute, the Swedish Environmental Protection Agency, the Swedish Association for Hunting and Wildlife Management and the Province of Arezzo.

Biomass estimation

To estimate the biomass intake, we used the Whole Scat Equivalents (WSE), which summarises the relative dry volume for a given food item within the scat sample (Angerbjörn et al 1999), for the Scandinavian data and the AV% for the Italian data. Yearly biomass ingested from the food items were estimated on the basis of the known relationship between prey biomass consumed per collectable scat produced, using three calculations; Floyd et al 1978, Weaver 1993 and Rühe et al 2003. Calculations are presented with the Floyd equation: $y = 0.383 + 0.02x$, Weaver equation: $y = 0.439 + 0.008x$ and Rüehe equation $y = 0.731 + 0.00406x$, where the x = assumed live weight of prey species and y = estimated biomass consumed per scat.

Prey preference

Manly's preference index, α_i is a useful measure for quantifying predator preference in selective predation as it includes a random number of prey types of both constant and changing prey densities. To investigate prey preference, Manly's Alpha preference index, also known as Chesson's index (Chesson 1978) was used: $\alpha_i = (r_i/n_i) * [1/\Sigma(r_j/n_j)]$ where prey type r_i or r_j is the proportion in the diet and n_i or n_j the proportion in the environment. Manly's alpha ranges from 0 to 1; r_i and r_j are the proportions (biomass) of prey type *i* or *j* in the wolf diet, n_i and n_j are the proportions (biomass) of prey type *i* or *j* in the environment. Unselective predation occurs if $\alpha_i = 1/m$ (*m* = total number of prey types). Prey species *i* is preferred if α_i is greater than $1/m$, whereas negative selection is found if α_i is less than $1/m$. Conversely, if $\alpha_i = 1/m$, less of prey type *i* occurs than expected by random feeding, i.e. prey type *i* is avoided by the predator.

Niche width

The calculations of niche width were based on seven prey groups in Scandinavia and eight in Tuscany. Levin's Food Niche Breadth (FNB) index (Levins 1968) was used to measure specialisation quantitatively for the wolf diet composition within Scandinavia and Tuscany as well as between the countries. Levin's index is defined as $B = 1/\Sigma p_j^2$ where p_j = proportion of fractions of items in the diet that are of food category *j.* Levin's Food Niche Breadth can be standardised and expressed in a scale from 0 to 1 with the help of an equation, $B_A = (B\text{-}1)/(n\text{-}1)$ where B_A = Levin's standardised FNB, *n* = number of possible resource states.

Niche overlap

To calculate niche overlap, Pianka's index (Pianka 1973) was used:
$O_{jk} = \Sigma (p_{ij} * p_{ik}) / [\sqrt{\Sigma p_{ij}^2 * \Sigma p_{ik}^2}]$ where O_{jk} is Pianka's measure for niche overlap between predator *j* and predator *k*, p_{ij} is the proportion of prey type *i* in relation to the total amount of prey ingested by predator *j*, p_{ik} is the proportion of prey type *i* in relation to the total amount of prey consumed by predator *k*, and *m* is the total number of prey types. The calculations were based on the relative biomass of the prey types. The index ranges from 0, i.e. no overlap, to 1, i.e. complete overlap.

Dataset accuracy

Graphical comparisons are always useful, and these can be supplemented by parametric or non-parametric tests to compare means and variances. The essential idea behind bootstrapping is that when the only information available about a statistical population consists of a random sample from that population, then the best guide to what might be obtained by resampling the population is provided by resampling the sample and we used R to produce confidence intervals around estimates of dietary composition (Reynolds & Aebischer 1991). A parametric bootstrap approach was used to calculate variances for the diet of each year, calculated 10,000 bootstrap estimates to obtain the standard error for the estimated

diet components and examined the mean of the bootstrap distribution to assess bias in the estimates (Efron and Tibshirani 1993).

4.4 Statistical analysis

When data was normally distributed, statistical significance was tested with independent samples *t* test, single factor or two-factor ANOVA without replication and post-hoc Tukey HSD test. When data was not normally distributed, I used Mann Whitney U and Kruskal-Wallis H tests and Spearman's rank correlation and Pearson's chi-square test. Statistical analysis was performed using the software SPSS (SPSS version 21.0, Inc., Chicago, IL, U.S.A.).

5 RESULTS AND DISCUSSION

5.1 FEEDING UNDER THE RISK OF INTRAGUILD PREDATION - PAPER I

Twenty-six moose carcasses were recorded during a total of 1 518 camera days including 4 008 photos of red foxes and 859 of pine martens in south-central Sweden. Twenty-one of the carcasses (representing 81%) were scavenged by red foxes and 10 (38%) by pine martens. Eight carcasses were scavenged by both red foxes (*N* = 2 496 photos) and pine martens (*N* = 838 photos) but the two species were never documented on the same photo. On 57 occasions (2%) at the 8 carcasses scavenged by both species, red foxes visited the carcasses after the pine martens had left and only on 8 (14%) occasions, within 1 hour (13-33 minutes). On 55 occasions (7%) pine martens visited the carcass after the red foxes and 14 (25%) of these occasions were within 1 hour (3-57 minutes). The time of visit by red fox and pine marten after a visit by the other species did not differ significantly (Mann Whitney U-test, U = 3.26, p = 0.071).

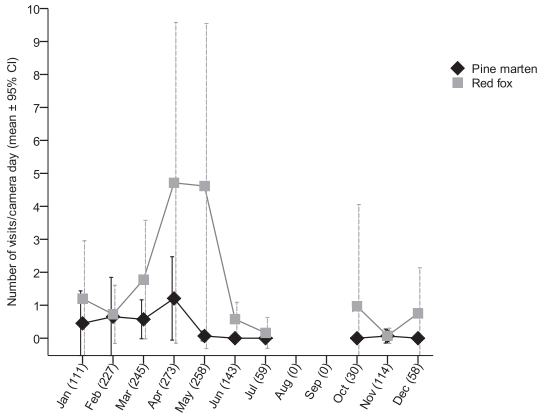

Fig. 1. Average number of visits to wolf-killed moose sites (*N* = 23) per camera day in relation to month (n-value is shown in parenthesis) and scavenging species (pine marten and red fox).

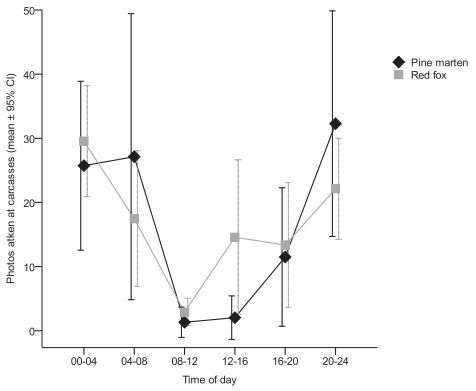

Figure 2. Daily scavenging pattern by pine marten (*N* = 850, 10 carcasses) and red fox (*N* = 3982, 21 carcasses) per wolf-killed moose. Scavengers were recorded by movement-triggered cameras in south-central Sweden, 2007-2009.

Pine martens visited carcasses mainly in January to April but rarely during the rest of the year. Red foxes showed the highest number of visits during spring (April to May, intermediate during winter and few during summer. The daily activity pattern differed significantly between pine martens and red foxes among the 6 time periods (X^2_5 = 124.153, P <0.001). Pine martens showed the highest activity between 20:00 and 24:00 whereas the red fox had the highest activity between 00:00 and 04:00. However, there was a positive overall correlation in the timing of visits, i.e. how these four-hour periods were ranked from highest to lowest activity (Spearman rank correlation, N = 6, Rho = 0.886, P = 0.048. The type of habitat at carcass sites (N = 26) significantly affected the presence of pine martens as there was a higher proportion of visits to carcasses in forests 21-60 years of age (70%, N = 10) compared to forests 0-20 years of age (15%, N = 13) and forests >60 years old. In contrast to pine martens, the presence of red foxes at carcasses was not affected by the type of habitat. As behaviour of the red fox might have been biased by the presence of the camera, we repeated the analyses of behaviour by excluding vigilant behaviour directed towards the camera for both species. To avoid bias from variation in the placement of the camera in relation to the carcass, we only used carcasses where both species were present for this analysis (N = 8, 3063 photos). Pine martens were more vigilant (30%) than red foxes (19%), they fed less (57%) than red foxes (72%), while other types of behaviour were almost equally frequent, pine marten (13%) and red fox (9%; X^2_2 = 58.170, P <0.001). Vigilance by red foxes was not affected by habitat characteristics while pine martens increased their vigilance by ~130% in habitats with high (open habitat) compared to low (dense habitat) visibility.

This study shows that red foxes visited a higher proportion of carcasses from wolf-killed moose and did so at a higher frequency than pine martens. This may be related to the broader habitat use and higher density of red fox compared to pine marten, which are more habitat-specialised. Habitat characteristics and visibility around feeding sites affected vigilance patterns more than the mere presence of a potential competitor and larger sized predator. We do not know if the higher vigilance by pine martens in open areas were caused by the presence of red fox. Presence of other predators like lynx, golden eagle and other birds of prey may also affect the behaviour of pine martens.

Carcass availability in a scavenger home range is affected by habitat composition as carcasses in preferred habitats will be more frequently used than carcasses in non-preferred habitats (Jędrzejewski and Jędrzejewska 1992; Gese et al. 1996, Selva et al. 2005). If the best feeding habitat also is the most risky, animals must make a trade-off between feeding and vigilant behaviour (Lima and Dill 1990). The restricted habitat use previously shown for pine martens (Pedrini et al. 1995) was also confirmed in our study as the location of the carcasses obviously limited their use. This pattern was not shown by red foxes which exploit a wider range of habitats (Weber and Meia 1996) and were unaffected by visibility around carcasses. Pine martens are known to avoid open areas due to the increased predation risk in these habitats (Brainerd and Rolstad 2002; Rondinini and Boitani 2002) and our

results showing increased vigilance in habitats with open compared to dense visibility confirm this pattern.

Table 3. Effects of habitat, visibility and coverage on the proportion of vigilant behaviour per feeding bout by pine marten (*N* = 69) and red fox (N = 227) at remains after wolf-killed moose (*N* = 15), using linear mixed model. The behaviour was recorded with movement-triggered cameras during October to July of 2007-2009.

Model	Explanatory variables	ß	SE	P	95% CI for ß	
					Lower	Upper
Pine marten	*Intercep*t	0.894	0.295	0.004	0.305	1.483
	Forest age – 60-120	-0.583	0.211	**0.007**	-1.005	-0.162
	Forest age – 21-60	0.001	0.208	0.994	-0.415	0.418
	Forest age – 0-20	0				
	Visibility – dense	-0.293	0.113	**0.012**	-0.519	-0.068
	Visibility – open	0				
	Coverage – dense	-0.318	0.114	**0.007**	-0.545	-0.091
	Coverage – open	0				
Red fox	*Intercep*t	0.410	0.123	0.001	0.168	0.652
	Forest age – 60-120	-0.131	0.137	0.343	-0.401	0.140
	Forest age – 21-60	-0.026	0.150	0.861	-0.322	0.270
	Forest age – 0-20	0				
	Visibility – dense	0.109	0.106	0.302	-0.099	0.318
	Visibility – open	0				
	Coverage – dense	-0.011	0.152	0.943	-0.310	0.288
	Coverage – open	0				

The almost similar daily activity pattern of carcass use shown by pine martens and red foxes did not support the idea of a crepuscular or diurnal activity pattern by pine martens to avoid red foxes. However, the daily peak of activity was in the early night for pine martens, whereas red fox activity peaked late at night. As pine martens were not proportionately more vigilant during time periods when red foxes were most active, this suggests that they may not perceive the increased risk of encounters with red foxes as requiring a major change in their feeding behaviour. Also, there may be an interspecific transfer of information in sympatric carnivores as to the whereabouts of good feeding opportunities (Krebs and Dawkins 1984), as for example when foxes are reported to follow badgers to good foraging sites

(Macdonald 1987). In this study, we once recorded a red fox and badger feeding together at the same carcass, but never red foxes and pine martens.

Pine martens exhibited an upright posture during one third of their vigilant time, thus very likely making a trade-off between time devoted to overt vigilance and consumption as an anti-predator strategy. For red foxes, only one type of vigilant behaviour occurred according to the photos taken. The lower level of vigilance shown by red foxes may be a direct response to several generations of zero or negligible wolf presence in Scandinavia (Wabakken et al. 2001), albeit there has always been a predation risk from lynx and birds of prey. This may have caused red foxes to underestimate the predation risk from the re-establishing wolf population, as has also been shown in moose behaviour (Sand et al. 2006*a*). At temperate latitudes such as in northern and central Europe, large herbivore carcasses are usually available for very long time periods during the cold season (Selva et al. 2003). Red foxes and pine martens continued to use carcasses several months after the time of death, suggesting that scavenging on wolf-killed moose constitutes an important food resource for these species. This may be especially important during spring, which usually is a critical period for survival and growth of reproducing animals and their new-born offspring (Clutton-Brock 1988). The slightly earlier seasonal utilization period in scavenging by pine martens compared to red foxes in our study may reflect that the time of parturition for red foxes occurs slightly later in spring (April to May; Lindström 1981) than for pine martens (March to April; Zalewski 2001) which thus correlated with periods of activity peak at carcass sites.

The growing Scandinavian wolf population will likely benefit both the red fox and pine marten populations through increased food supply during certain/critical times of the year.

5.2 PREY SELECTION IN NORTHERN AND SOUTHERN EUROPEAN WOLVES - PAPER II

From 2159 scats from 17,370 km^2 in south-central Scandinavia and 542 scats from ~8000 km^2 in Tuscany, wolf diet composition is clearly dominated by wild ungulates. The remaining minor categories were, in the order, small mammals and vegetation in Scandinavia and vegetation and domestic animals in Tuscany. In terms of biomass intake, Sandinavia had the highest biomass found in wild ungulates 97.3% and minor parts from small mammals 2.46% and domestic animals 0.24%. Tuscany also had the highest level of biomass found in wild ungulates 94.76%, followed by domestic animals 4.35% and small mammals 0.89%. Our data shows wide variations in seasonal prey age class variation where in Scandinavia, a two-tailed Mann-Whitney test shows significant increase in selection of moose calves: U = 1,443.5, n = 216, 18, P =0.05, compared to Tuscany, where all cervid fawns increased in summer (U = 2.5, n = 7, 1, P <0.564), as did adult fallow deer and adult mouflon (U = 2.0, n = 3, 2, P =0.519). Calves offer a relatively small amount of biomass per kill which results in a higher kill rate per time unit during the vegetative growth period. However, body size increases rapidly resulting in higher biomass intake per kill for predators. Using Manly's alpha preference index, wolves in Scandinavia clearly showed positive preference of moose and negative preference of roe deer and wolves in Tuscany showed positive

preference of wild boar and mouflon and negative preference of roe deer, red deer and fallow deer. Levin's Food Niche Breath was broader in Tuscany (B = 4,0) than in Scandinavia (B = 2,5) and consequently higher standardised in Tuscany (B_A = 0.23) than in Scandinavia (B_A = 0.12). This results in a higher niche overlap in Scandinavia (O_{jk} = 0.85) than in Tuscany (O_{jk} = 0.63) using Pianka's index.

Moose was the main prey in Swedish wolf diet, having the highest density values (1.26/km^2) compared to roe deer (0.57/km^2). The most abundant prey species was however not selected in Tuscany where the most common prey species, wild boar, had only one third of the density (6.91/km^2) compared to the second selected prey species, roe deer (25.1/km^2). In Alpe di Catenaia, wild boar was also heavily hunted by humans, resulting in fewer individuals available for wolves. Nonetheless, wild boar was the most selected prey species there but not in the two other Tuscan areas.

Tabel 1. Assumed prey weight, Whole Scat Equivalence/average volume and estimation of consumed biomass in kg and per cent in south-central Sweden and Tuscany calculated using the Weaver equation (Weaver 1993) during summer May-September in Sweden and winter October-April in Italy.

	Summer					Winter				
SWEDEN	assumed weight (kg)	WSE / AV%	biomass consumed/scat (kg)	biomass consumed (kg)	biomass consumed (%)	assumed weight (kg)	WSE / AV%	biomass consumed/scat (kg)	biomass consumed (kg)	biomass consumed (%)
moose	116,7	78,7	1,37	1102,2	29,8	192	85,3	1,98	2248,4	95,2
roe deer	17,1	8,6	0,58	462,4	12,5	20	10,5	0,60	83,9	3,6
beaver	18	1,6	0,58	468,1	12,7	18	1,1	0,58	8,4	0,4
hare	3,5	2,7	0,47	375,0	10,2	3,5	0,3	0,47	1,8	0,1
badger	10,5	1,5	0,52	420,0	11,4	10,5	0,1	0,52	0,6	0,0
domestic	25	2,0	0,64	513,1	13,9	25	1,0	0,64	8,0	0,3
rodents	0,025	4,9	0,44	352,7	9,5	0,025	1,8		10,3	0,4
				3693,5					2361,5	
TUSCANY										
wild boar	36,1	36,1	0,73	70,5	38,3	33,8	51,52	0,70	100,1	53,2
roe deer	27,8	24,7	0,66	43,7	23,7	24,6	29,57	0,60	51,5	27,4
red deer	39,1	7,6	0,75	15,4	8,4	102,5	2,93	1,30	10,1	5,4
fallow deer	23,9	15,6	0,63	26,3	14,3	55,4	6,17	0,50	7,7	4,1
mouflon	22,9	10,1	0,62	16,9	9,2	23,8	5,96	0,60	10,3	5,5
hare	3,0	0,8	0,46	1,0	0,6	3	0,63	0,50	0,8	0,4
rodents	0,0	1,3	0,44	1,6	0,9	0,03	0,1	0,40	0,1	0,1
domestic	55,8	3,7	0,89	8,8	4,8	55,8	3,13	0,90	7,6	4
				184,2					188,3	

Generated changes in prey composition and density and strongly different ungulate communities of the three areas in Tuscany which changed through the years, resulted in higher variance compared to Scandinavia. Karlsson et al (2007)

analysed wolf habitat variables and determined that there was a significant decline in the proportion of built-up areas within the wolf territories, but no significant change for open land or local road density. The Apennine ecosystem is changing in recent decades due to abandonment of traditional farming and forest activities and the increase in forest coverage which benefits ungulates as well as wolves that prefers areas with high forest cover, few roads and low human density (Mech et al 1988). The wolf habitat is more dynamic in the sense of landscape changes and increase of prey abundance. These are positive changes for the wolf population and the co-existence with the dense human density is somewhat eased in the Tuscan Apennines. Different latitudes may reflect on habitat heterogeneity, however, the level of human utilisation of the landscape determines wolf diet diversification too. The intensively exploited forest industry in Scandinavia prevents rich species diversity, opposing to the abandoned former agricultural areas in the Apennines, allowing re-forestation and species diversification. The outcome may lead to increased variation in predator-prey relationships due to a more extensive heterogeneity in Tuscany compared to south-central Scandinavia.

The body size difference in Swedish and Italian wolves was not the only reason for Italian wolves predating on smaller ungulate species, wild boar in Italy are relatively small compared to northern European. No larger ungulates than red deer are present in Tuscany and by choosing young wild boar during winter may suggest that they are not only preferred due to lack of experience and anti-predator behaviour. Optimal foraging strategy, described by Stephen and Krebs (1986), highlights the importance of predators' selection of the most profitable prey, profitability being the ratio between energy gain and handling time. Within a prey species, there are differences in sex-, age- and size groups which affects kill rate and risk of injury. Adult wild boar can cause serious injury or death to predators, and it can be energy beneficial targeting younger individuals. Roe deer is the second prey selection as well as the second largest source of biomass in both south-central Scandinavia and Tuscany with the exception of summer in Scandinavia. When present at high density, roe deer can be a profitable prey for wolves because of the high encounter rate and low handling time (Huggard 1993; Mattioli et al 2004; Sand et al 2005), nevertheless, roe deer selection was low in Tuscany in relation to their density which was higher than wild boar. Higher human density in Italy results in higher depredation but the reason for this may well be the different approaches of animal husbandry, not prey abundance and density.

5.3 SCAVENGER TEMPORAL AND SPATIAL PARTITIONING IN NORTHERN AND SOUTHERN EUROPEAN WOLF TERRITORIES - PAPER III

Cameras recorded at 67 carcasses from February 2006 to June 2010 in south-central Sweden and at 137 carcasses/feeding sites from July 2010 to May 2013 in Alpe di Catenaia, in the Tuscan Apennines, hereafter abbreviated SWE and IT. Visiting scavengers in SWE was the red fox, common raven, pine marten, jay,

goshawk, golden eagle, crow, wolf, magpie, badger, brown bear, domestic dog *(Canis familiaris)*, wild boar and only a few visits by eagle owl, sea eagle, wolverine and lynx. The most active scavengers were *Corvidae* spp. 48.4% followed by red fox 27.7%, birds of prey 11.1%, pine marten 8.3% and wolf 2.3%. In IT, the red fox, marten, badger, dog, wolf, wild boar, wildcat, bird of prey, *Corvidae* spp. and polecat. The most active visitors were wild boar 44.4%, red fox 38.7%, marten 6.9%, dog 2.4% and wolf 2.4%. We compared individual visiting occasions of exclusively common mammalian scavenging species (red fox, marten, badger, wolf, wild boar) in SWE and IT, since avian scavenger visits were very rare in the latter area, which may indicate that this mountainous habitat is not strongly selected by birds of prey or *Corvidae* spp. We never recorded any intra-guild predation or attacks causing injury at the feeding sites, nevertheless, a few occasions when red fox chased away martens.

Within SWE and IT, Kruskal-Wallis test showed there was no significant difference in number of visiting occasions of the four species in SWE (H =0.14, n = 1076, 33, 318, 89, P = NS) or IT (H =6.95, n = 1843, 162, 346, 100, P = NS), but there was significant differences between the SWE species compared to the same specie in IT. Red fox differed between SWE and IT, a two-tailed Mann-Whitney exact test for two independent samples showed higher visiting occasions in IT than in SWE (P < 0.0001), as did marten (P = 0.019) and wolf (P < 0.0001). Badger showed no significant difference between SWE and IT being less frequent in the latter area.

Norhtern and southern European scavenger comparison

Comparing each specie, there was a significant relationship between red fox in SWE and IT in 24 hour activity pattern: Spearman's r_s = 0.886, n = 6, P = 0.019, but seasonal pattern P = NS, badger 24 h: r_s = 1.0, n = 6, P < 0.01 but seasonal NA, marten 24h: r_s = 0.9, n = 6, P = 0.037 and seasonal P = NS, wolf 24 h P = NS and seasonal: r_s 4 = -0.949, n = 4, P = 0.051, wild boar 24 h NA and seasonal P = NS. There was no significant relationship of feeding site selection related to visibility, snow coverage or vegetation coverage within the species in SWE and IT.

Site selection

SWE; vegetation coverage was high in 7.2% of the camera sites, medium in 57.0% and low in 35.8% of the visited camera sites. 87.1% of all photos were taken when camera sites were covered with snow and 12.9% no snow. Most scavengers preferred open areas with low vegetation and good visibility whereas badger and wolverine were always, and red fox most often, seen in dense vegetation with poor visibility. Snow coverage was predominantly used by red fox and raven, but also wolf, badger and wolverine preferred high snow coverage. Wild boar and lynx never appeared at sites with snow cover. 20.9% of the cameras were <1 km from human disturbance and only red fox (1.2% of their total visits) and magpie (7.4% of their total visits) visited these sites. IT; vegetation coverage was high in 15.0%, medium in 40.5% and low in 44.5% of the visits. Wolves, badgers and avian scavengers preferred low vegetation and good visibility. Without snow coverage, red fox and

wild boar appeared equally but when snow coverage at the site, red fox was the most active visitor. Avian scavengers seldom appeared when there was snow coverage and of mammals, nor did marten. 15.4% of the cameras were <1 km from human disturbance and avian scavengers appeared most of all with 100% of the *Corvidae* spp. visits, whilst red fox was the most common mammal with 39.2%.

Habitat features influences scavenging species feeding behaviour (Hunter et al 2007), however, air temperature exceeding 17°C has probably the strongest effect on carcass fate as insects and arthropods will rapidly speed up decomposition (DeVault et al 2004). The longer summer period with higher temperatures in the IT contributed to faster decomposition, but also of scavenging behaviour clearly shown in wild boar. Wild boars selected the rich supply of insects and arthropods during the warm period and the access to food items not covered by snow was easy during the cold period, suggesting that there was not as high demand for alternative and supplementary food sources such as carrion as seen in Sweden.

SWE has more light per 24 hours during the summer season and less during the winter season compared to Italy, which can bias the result when classifying equivalently. Hours of light differ with latitude and that this should be acknowledged when comparing activity in these two areas. Figure 1 clearly shows the similar 24 h activity pattern of scavengers, somewhat delayed in the Tuscan area compared to SWE, and the dissimilarity in the seasonal activity pattern. The resting period begins and ends earlier in northern European climate conditions.

Good visibility and low vegetation coverage was not important in Swedish wolves, but rather important for the Tuscan wolves. Red fox selected poor visibility with high vegetation in SWE but somewhat the opposite in IT. Only lynx and pine marten in SWE and wildcat, and martens in IT chose poor visibility and high vegetation. Seasonal differences in red fox activity may be explained by the large portion of berries during autumn in SWE. There was also a quite low number of visits by badgers in SWE and all occurred in late winter as did most of the visits in IT. This may be explained by their preference of earth worms (Goszczynski et al 2000) which are not as accessible as the earth crust is frozen during late winter, particularly in SWE. Martens had a similar pattern except for in late winter when in IT with less scavenging, most likely due to earlier spring and reproduction period when shift to other food resources.

The lowest scavenging activity in wolves in SWE was seen in late winter may indicate that they are not typical scavengers. Previous studies have shown nocturnal wolf activity in southern Europe (Vilà et al 1995; Ciucci et al 1997) due to centuries of persecution, but the spatial and temporal avoidance of humans is an adaptation in each geographic region (Kaartinen et al 2005; Theuerkauf et al 2003c; Theuerkauf et al 2007). As seen in the wolf diet study (Paper II), lower scavenging in early to mid-winter in the Tuscan Apennines, may be the result of wild boar juveniles being easy to catch due to lack of anti-predator behaviour and experience. Hunting a 10-35 kg prey animal with low risk of injury may be preferred instead of scavenging during that time period, however, the IT wolves followed the common scavenging patter with the peak in late winter.

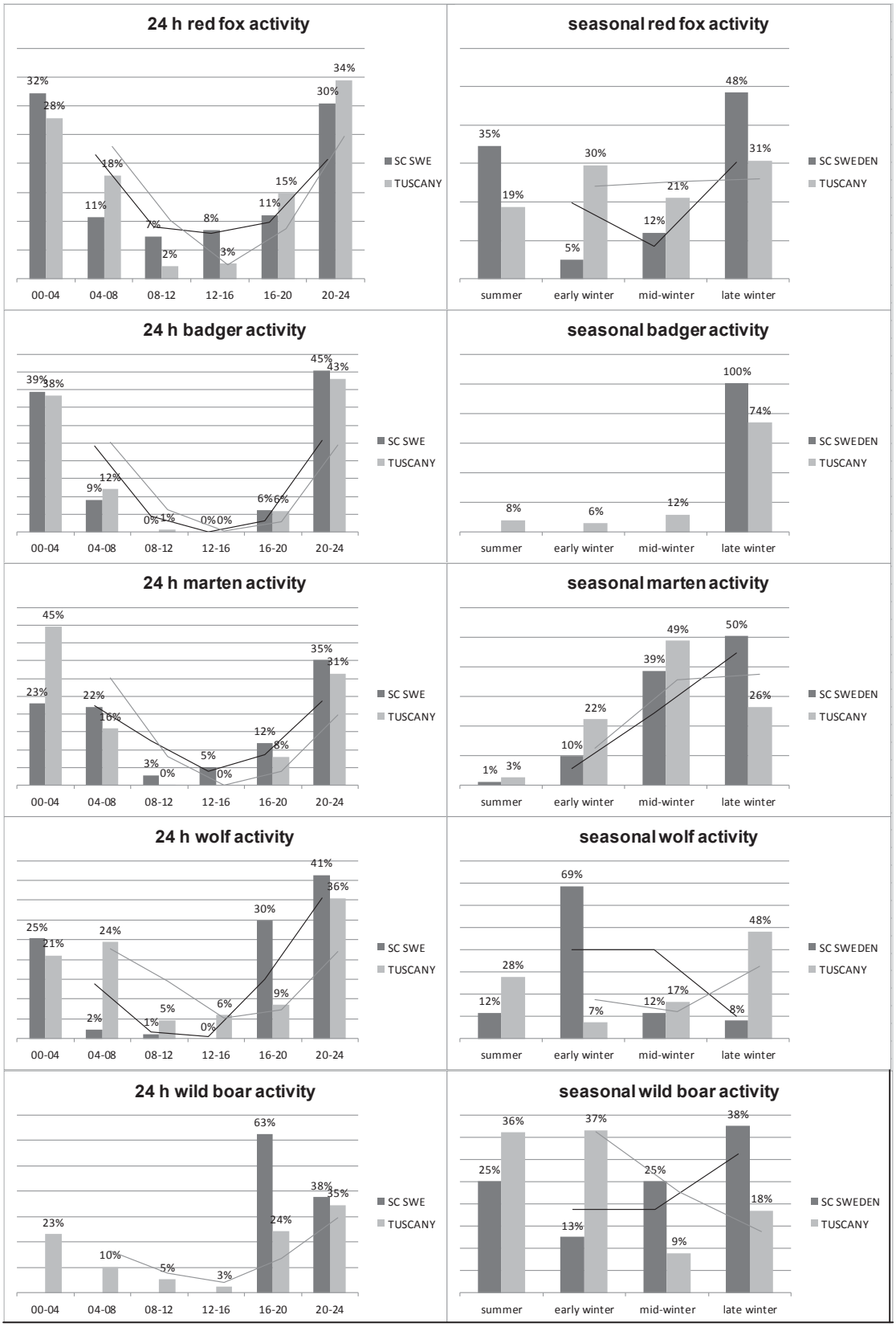

Fig. 1 24 h and seasonal temporal activity pattern in red fox, badger, marten, wolf and wild boar in South-central Sweden and Tuscan Apennines.

5.4 THE FUNCTION OF VIGILANCE IN AN APENNINE WOLF TERRITORY – PAPER IV

Seventeenspecies were recorde during 35 months a wolf territory in Alpe di Catenaia. Totally 5366 visiting occasions were calculated whereof scavengers; wild boar 38.2%,red fox 34.5%, marten 6.1%, badger 2.8%, domestic dog *(Canis familiaris)* 1.9%, wolf 1.6%, *Corvidae* spp. 0.09%, bird of prey 0.09%, polecat *(Mustela putorius)* 0.09% and non-scavengers; porcupine 1.5%, wildcat 0.3%, roe deer 10%, red deer 0.3%, hare 1.6% and red squirrel *(Sciurus vulgaris)* 0.03%. It was visually impossible to distinguish between pine marten and stone marten why both were classified as 'marten'. Domestic dog visited mainly daytime during autumn and winter when wild boar hunting season took place and avian scavengers were very rare.

Scavenger guild members interaction or interference

Two or more individuals of different species visited the sites simultaneously very rarely but when a scavenger appeared within 180 min after the previous had left, it was recorded. Marten and fox withdrew immediately when the superior scavenger appeared. Foxes followed marten at 51 occasions, between 0-168 min after marten had left (average 77 min), but martens followed fox in 40 occasions, from 0-134 min (average 48 min) which in a Mann-Whitney test, is significantly closer to when the fox has left the site than vice versa: U = 761.5, n = 51, 40, P = 0.039. The other scavengers following other scavengers are seen in Fig. 2, however, none of these showed sifnificantly more rapid than the marten.

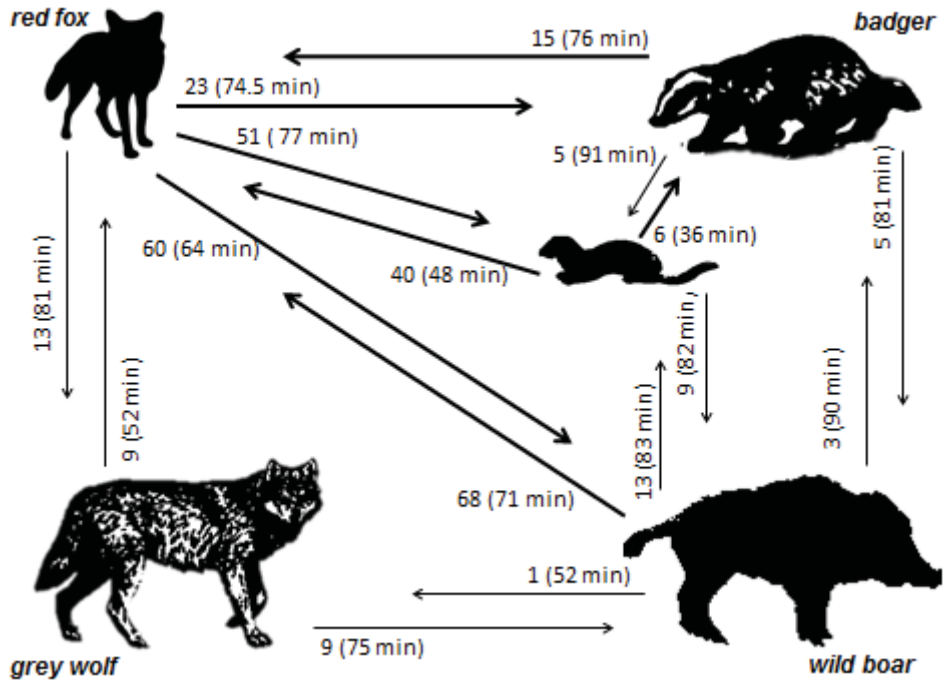

Fig 2. Number of observations when scavengers follow other scavengers and average minutes after the previous visitor has left the carcass/feeding site.

Behaviour at feeding site

A Kruskal-Wallis test shows significant difference in scavenger behaviour at feeding sites: H = 11.96, n = 8072, 214, 1104, 152, 4031, P = 0.018. Each scavenger's distribution of different behaviours is visually demonstrated by percentage of total behaviour at feeding sites in Fig 3.

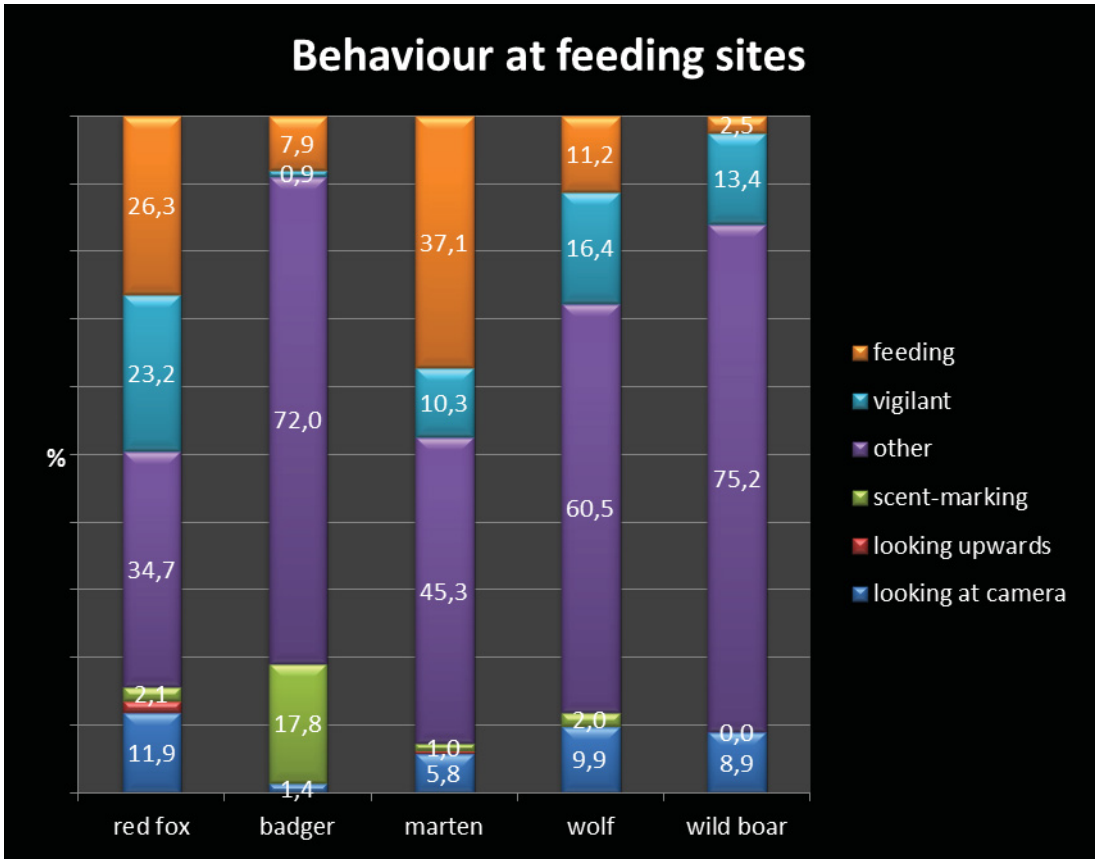

Fig 3. Behaviours at feeding sites were defined as *Feeding* - chewing, *Vigilant* - a head lift which interrupts feeding activity on the carcass, followed by visual scanning of the environment, *Looking upwards* - raising head toward tree canopy or sky, *Scent-marking* - urinating, excavating or rubbing side of head and/or neck on ground or vegetation, *Looking at camera* - eyes focusing directly on the camera, *Other* - inspecting, searching, social interaction (mostly wild boar and fox), moving, grooming (only fox and marten)

For estimating if the two most active scavengers, red fox and marten, differed in behaviour with other areas we tested vigilance against Swedish data, and no significant difference was found. Temporal and spatial activity pattern and selection is described in Paper III, and here we looked at the anti-predator behaviour in the scavenger guild. No significant difference in feeding site selection related to visibility (Mann-Whitney: U = 20, n = 7,7, P = 0.565), snow coverage (U = 15, n = 7,7, P = 0.224) or vegetation coverage (Kruskal-Wallis: H = 1.452, n = 7,7, P = 0.484) in any of the scavengers. Other factors affecting anti-predaotr behaviour may be crepuscular hours and the moon cycle. No significant preference between dusk and dawn by the scavengers, Mann-Whitney: U = 7.5, n = 6, 6, P = 0.086. Scavengers showed no significant preference between full and new moon illumination (Mann-Whitney: U =

12, *n* = 5, 5, *P* = NS), nor was it shown when only comparing red fox and marten (Mann-Whitney: *U* = 2, *n* = 2, 2, *P* = NS). However, there are two characteristic features when classifying diurnal, nocturnal, crepuscular and moon illumination preference; martens preference of new moon with low moon illumination and wolf preference of morning twilight.

Red fox were clearly the main scavenger with most visiting occasions, showing the highest vigilance reflected in the behaviour of observing the camera most often of all the scavengers. Noticeable was also the behaviour of looking upwards towards the tree canopy or sky in spite of the very low precence of avian predators. Red fox are known to kill martens (Lindström et al 1995), but this behaviour appeared in combination with strong vigilance and most often when no martens had been observed before or after the red fox visit. They were mainly nocturnal but showed no attraction to crepuscular hours or lunar illumination even if somewhat more in full moon than new moon. Several red fox individuals showed injuries such as limp and lost legs and eyes, which may indicate that they live under high predation pressure from solely wolf or both wolf and domestic dogs.

In Alpe di Catenaia, badgers did not feed on carcasses often, lacked vigilant behaviour as the only superior scavenger and possible predator is the wolf, but scent-market more than any other scavenger. Badgers followed red fox, which has been seen in previous studies (Macdonald 1987), and a few times also marten. They are mostly nocturnal and visited somewhat more sites during new moon than full moon.

Pine and stone martens were the second most active scavengers which followed and was followed by red fox and badger. They arrived at feeding sites more rapidly than other scavengers after the previous visitor had left. They spend most time feeding and next after badger, the least vigilant, nonetheless, the smallest scavenging species. Entirely nocturnal and seem to prefer the darkness of new moon rather than full moon illumination. Contrasting to other studies where foraging is restricted and adjusted due to predation pressure (Lima and Valone 1986), marten did not expressed a trade-off in foraging and anti-predator behaviour compared to other scavengers.

Wolves scavenged moderately (11.2%) compared to the other scavengers in this study and to Swedish wolves (37.2%)(Ståhlberg, unpublished). Wolf followed only red fox and wild boar at a few occasions, and it is difficult to determine whether it was in search of carcasses in the case when after red fox, or after prey as wild boar is the main prey in Alpe di Catenaia (Davis et al 2012; Paper II). They were next after red fox, the second most vigilant scavenger. They were mainly nocturnal but also active during morning twilight until noon.

Body size did not determine whether scavengers follow each other or not, as martens were the quickest specie to arrive after other species had left a carcass. The low numbers of avian predators in the Tuscan Apennines did not generally result in lower vigilance in scavengers compared to Sweden where ~4.5% of the scavengers are birds of prey (Paper III). When comparing vigilance behaviour in Sweden and Italy (Paper I), red fox (19 and 23%), badger (0 and 1%) are rather similar, while marten

(37 and 10%) and wolf (7 and 16%) differed vividly. Feeding behaviour at carcasses was dominated by marten, vigilance (including looking upwards and at the camera) by red fox and scent-marking by badger and conclusively, martens balance the trade-off between feeding and vigilance in the most beneficial structure.

Riala territory 2010

PAPER I

Feeding under high risk of intra-guild predation: vigilance patterns of two medium-sized generalist predators

CAMILLA WIKENROS,* SOPHIE STÅHLBERG, AND HÅKAN SAND

Grimsö Wildlife Research Station, Department of Ecology, Swedish University of Agricultural Sciences, SE-730 91 Riddarhyttan, Sweden (CW, HS). Department of Natural and Environmental Science, University of Sassari, Via Muroni 25, Sassari 07100, Sassari, Italy (SS).

To balance conflicting demands for food and safety from predation, foraging animals trade-off time between feeding and safety by vigilant behaviour. We studied the behaviour of the red fox *(Vulpes vulpes)* and pine marten *(Martes martes)* scavenging at carcasses from moose (*Alces alces*) killed by wolves (*Canis lupus*) in Sweden. The red fox was observed visiting carcasses more often and at a higher frequency than the pine marten which restricted carcass use to certain habitats. Both species followed a similar daily and seasonal activity pattern. The seasonal peak of scavenging, in April for pine martens and April-May for red foxes, shows that remains after wolf-killed prey are likely an important food sources for both these species during the reproductive phase of the year. Pine martens displayed an overall higher level of vigilance and a lower level of feeding than red foxes. Vigilance by pine martens was affected by habitat, visibility and vegetative coverage at carcass sites. Pine martens did not display increased vigilance during time periods of high red fox activity and there was no effect of the time of day. Our study shows some support for the importance of interspecific predation risk leading smaller sized predators to trade-off foraging for increased vigilance but habitat characteristics affected vigilance patterns more than the mere presence of a larger sized predator.

Key words: intermediate predators, intra-guild predation, *Martes martes*, scavenging, sympatric predators, vigilance, *Vulpes vulpes*

Ecosystems consist of several levels which integrate through complex trophic dynamics and community organisation. Predator species can be regarded as having different roles in different areas, e.g. as a top predator in one location but as a mesopredator in another depending on the co-occurrence with other predators. It has been suggested that smaller, subordinate species coexist with larger, dominant guild members through temporal partitioning of habitats and resources (Pianka 1974; Harrington et al. 2009). In multi-predator communities, competition or predation limits mesopredator abundance as many individuals suffer a reduction in fecundity, survivorship or growth as a result of intra- or interspecific resource competition or direct interference competition (Watts and Holekamp 2008). Food choice, habitat selection and time have been suggested as being the most important niche dimensions in interspecific resource partitioning (Pianka 1969; Schoener 1986; Ritchie and Johnson 2009), but recent studies have shown that it may be more complex than previously considered (Cozzi et al. 2012). Periods with increased levels of interspecific competition are expected to foster niche narrowing, and sympatric species are therefore expected to reduce their resource overlap by selecting different

habitats, shifting to different diets, or displaying different patterns of activity (Guthrie and Moorhead 2002). Predation by top predators on intermediate predators reduces competition through a numerical effect on the intermediate predators, but should also lead to a change in the behaviour of the targeted species (Kimbrell et al. 2007). Vigilance is typically related to anti-predator behaviour by reducing the predation risk at the expense of time spent foraging (Caro 1987; Rasa 1989) and has thus an immediate effect on fitness.

Mammalian predators confront many natural threats, including both intra-guild predation and food theft (kleptoparasitism), by members of their own and other species (Caro and Stoner 2003). The most frequently described interspecific predation among mammalian predators involves canids and felids as the aggressors and smaller-sized canids, felids or mustelids as the victims (Palomares and Caro 1999). The red fox (*Vulpes vulpes*) and the pine marten (*Martes martes*) are two common small to medium-sized sympatric carnivores in the boreal ecosystem. Whereas these two species commonly share the same food resource (Lanszki et al. 2007), the red fox actively pursues and kills pine martens to the extent that predation by red foxes has been documented as limiting their population growth (Lindström et al. 1995). Foxes exploit the widest range of habitats (Weber and Meia 1996), whereas the pine marten is more selective regarding forest age, composition and structure (Lindström 1989; Brainerd and Rolstad 2002; but see review in Virgós et al. 2012 that indicate a greater habitat flexibility) and avoids open areas with increased risk of predation (Storch et al. 1990; Brainerd and Rolstad 2002; Rondinini and Boitani 2002). In the context of interspecific competition, the pine marten as a habitat specialist, in combination with its smaller size, has the role of the subordinate species in relation to the red fox. Thus, these two species serve as good study objects for investigating the importance of interspecific predation risk on vigilant behaviour where intra-guild predation may result in resource partitioning and niche differentiation (Rosenzweig 1981; Ricklefs et al. 1990).

Scavenging may be an alternative food resource for carnivores during times of prey shortage, under stressful environmental conditions, or during other critical periods. Both red foxes and pine martens may therefore benefit from utilizing carcasses of prey killed by larger predators. In this study, we investigated whether differences in predator size affect the pattern of predator scavenging and behaviour. Specifically, we examined scavenging pattern of red foxes and pine martens at wolf-killed *(Canis lupus)* moose *(Alces alces)* in terms of frequency of visits, and daily and seasonal activity pattern. We also investigated patch use and fine scale behaviour when feeding by pine marten and red fox with particular interest in vigilance. We hypothesize that the red fox is the dominating scavenger as indicated by the frequent killing of pine martens (Lindström et al. 1995) in combination with the more restricted use of habitats demonstrated by the pine marten (Brainerd and Rolstad 2002; Rondinini and Boitani 2002). If predation by red foxes constitutes a major limiting factor for pine martens access to carcasses we predict that the activity pattern of the pine marten would be different from the one used by the red fox. Also, we predict that pine martens vigilance at carcasses would be related to the probability of encounters with the red fox. Finally, we predict that the location of carcasses in relation to habitat is more important for the pine

marten than for the red fox, a pattern that not necessarily need to be linked to the predation risk by red foxes on pine martens. If we do not find evidence for that the pine marten adjust their behaviour according to the presence of red fox we regard it as unlikely that the red fox poses a major factor for shaping the feeding pattern and behaviour of pine martens. We used data on behaviour of red foxes and pine martens collected by motion triggered cameras mounted close to carcasses of moose killed by wolves.

MATERIALS AND METHODS

Study area - The study was carried out in eight wolf territories in south-central Sweden (59-61ºN, 12-16ºE). Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*) were the dominant tree species, and birch (*Betula pubescens, B. pendula*) and aspen (*Populus tremula*) occurred in various mixtures. Most of the forests are managed for a mosaic of stands of different age classes. The climate is characterized by continental climate with average temperatures of -5 °C in January and 15 °C in July (Vedin 1995). The ground is usually snow covered between late November and early April with a mean snow depth of 20 cm in mid-January (Dahlström 1995). The time period with days with frost is mid-September to mid-May (Dahlström 1995).

In the 1980s, the pine marten population increased and expanded to areas where they had not been previously observed (Storch et al. 1990). During the same period, the density of the red fox population decreased dramatically due to an epizootic of sarcoptic mange (Lindström 1991). The present red fox population in Sweden includes approximately 150 000 individuals and the pine marten population approximately 100 000 individuals (Swedish Association for Hunting and Wildlife Management 2010).

Wolves successfully reproduced in south-central Scandinavia (Wabakken et al. 2001) in 1983 and during the 1990s the wolf population increased in both numbers (29% yearly increase; Wabakken et al. 2001) and range, and in the winter of 2008/09, the total population in Sweden was estimated to be 166-185 wolves (25 packs and 11-15 pairs; Wabakken et al. 2009). Moose is the main prey both in number and biomass for wolves throughout the year (Sand et al. 2005, 2008).

Recording scavenging species - We used two different camera systems ("STC-WD2-IR" [Stealthcam, Grand prairie, TX, USA] and "Superkameran-II" [LOKE Special Electronics, Skinnskatteberg, Sweden]) to record scavenging pattern of red foxes and pine martens at remains after wolf-killed moose, during October to July, 2007-2009. The camera "Superkameran-II" was programmed to take 1 photo per minute irrespective of movement with invisible infrared light during night-time. Cameras (STC-WD2-IR) were programmed to take 3 photos with 1 second intervals every minute when triggered by movement. As red foxes initially reacted to the weak visible infrared light used in the original cameras, the light emitters were switched to emitters with a longer wavelength creating invisible infrared light (LOKE Special Electronics, Skinnskatteberg, Sweden) to avoid the effects of the light during night-time. We did not use photos from cameras with the original light emitters. In the analysis, we used 1 photo per minute, and for the camera brand "STC-WD2-IR" we used either the first photo taken, or if this was empty, the first photo with an identified animal present. Date and time were registered on all photos.

The Swedish Animal Welfare Agency approved camera monitoring of scavenging species (Permit Number: C 51/9). Permission for camera monitoring of moose carcasses on both state-owned and privately owned land was obtained from the County Administrative Boards in Sweden (Dalarna (Permit Number: 211-14304-2006), Gävleborg (Permit Number: 211-1371-09), Värmland (Permit Number: 211-15846-06), Västmanland (Permit Number: 211-11827-06), and Örebro (Permit Number: 211-03990-2006)).

Carcasses of moose were found during field visits of locations from GPS-collared wolves (according to methods described in Sand et al. 2005) or reported from the public. All procedures including capture, handling and collaring of wolves fulfilled ethical requirements and was approved by the Swedish Animal Welfare Agency (Permit Number: C 281/6, see Sand et al. 2006b). Cameras were set up after wolves left their kill (>2 km away from the carcass, Sand et al. 2008). We mounted cameras in trees approximately 0.5 m above ground and 2 to 4 metres away from the carcass. The proportion of edible biomass consumed was visually estimated at the time of camera set up. Cameras were checked once a month to change memory cards and batteries and were removed when edible parts of carcasses were totally consumed. The number of days a carcass was recorded was set to the time between camera set up and removal of the camera, excluding days with malfunction of the camera system.

Scavenging pattern and activity - We defined the number of visits as the number of photos with one-minute interval accounting for the number of individuals per photo. We calculated the frequency of visits as number of visits per camera day per month. To investigate daily activity pattern we divided daily 24-hour periods into six different time periods (00-04, 04-08, 08-12, 12-16, 16-20, 20-24) according roughly to day and night light. We used Pearson's chi-square test to analyse if the proportion of photos taken of pine martens and red foxes at carcasses differed between the time periods. A Spearman rank test was used to test for a correlation in presence between the two species among time periods.

Patch use - We classified each carcass site according to the prevailing habitat type such as forest with age classes 0-20, 21-60, 61-120 years or other habitats (such as lake or mire). Coverage by vegetation above the carcass was estimated by visual estimation of the percentage of cover in two categories: open (0-69%) or dense (70-100%). Horizontal visibility of carcasses was estimated from the four cardinal points by measuring the distance from where a carcass could be detected. This was done at 1.7 m height because sighting distance at the level of the scavengers may have differed during the camera recording time period due to height and cover by vegetation. Visibility was calculated as the average of all distances in the four directions and categorized as dense (0-14 m) or open (≥15 m). Coverage and visibility were measured at the time of camera removal to minimize disturbance when carcasses were being recorded. The effect of occurrence of red foxes at carcasses and type of habitat on the presence of pine martens at carcasses was tested using logistic regression. We also tested the effect of habitat on the presence of red foxes at carcasses using logistic regression. To test if the number of visits per carcass per camera day by pine martens was negatively affected by the number of visits by red foxes, we used linear regression.

Behaviour when feeding - We classified the behaviour of animals in the

photos in three categories: feeding, vigilant, or other behaviour. Feeding was defined as a lowered head close to the carcass and vigilance as when the animal's head was raised in an alert position (Atwood and Gese 2008). Photos of animals moving in or out of the picture, climbing trees (pine marten only) or unknown behaviour were classified as other behaviour. Differences in behaviour was analysed with Pearson's chi-square test (photos from all carcasses pooled). Using camera equipment may affect the behaviour of the study species (Cutler and Swann 1999, Swann et al. 2004). Therefore, we determined how often red foxes and pine martens looked in the direction of the camera as well as the other three cardinal points. Pearson's chi-square test was used to analyse if red foxes and pine martens looked in the direction of the camera significantly more than expected (25%) when vigilant, indicating that the animals reacted to the presence of the camera.

A linear mixed model was used to analyse the effect of fox activity and time of day on the vigilance of pine martens. Vigilance by pine martens was measured as the proportion of photos classified as vigilant behaviour per time period (as defined above and pooled for each carcass) and arcsine square root-transformed to achieve a more normal distribution. We only used time periods with a minimum of 5 photos. Fox activity was classified as a continuous variable as the number of photos taken per time period per carcass. Fox activity and time of day was used as fixed factors whereas carcass ID was equal to the random effect that assesses variation among carcasses.

Finally, we also tested for differences in vigilance by calculating the proportion of vigilant behaviour per feeding bout by pine martens and red foxes using linear mixed models with habitat, visibility, and coverage as fixed factors and carcass ID as a random factor. We defined a feeding bout as all photos taken within a maximum of 15 minutes from the previous. We only used feeding bouts with a minimum of 5 photos taken and calculated the proportion of vigilant behaviour and arcsine square root transformed the dependent variable to achieve a more normal distribution. Statistical analysis was performed using the software SPSS (SPSS version 21.0, Inc., Chicago, IL, U.S.A.).

RESULTS

Twenty-six moose carcasses were recorded during a total of 1 518 camera days. The median number of days for camera set up was 4 days after a moose was killed (range 1-15). On average 60% (range 10-90) of the total available moose biomass was consumed at the time of camera set up. The recording time period averaged 58 camera days (range 4-238) excluding 111 days (range 2-25) of recording at 10 carcasses with periodical malfunction of the camera system. A total of 15 463 photos were taken of which 11 756 were photos of identified scavenging species including 4 008 photos of red foxes and 859 of pine martens. Nine photos of pine martens and 26 photos of red foxes where more than 1 individual was present were excluded from the analysis of behaviour.

Scavenging pattern and activity – Twenty-one of the carcasses (representing 81%) were scavenged by red foxes and 10 (38%) by pine martens. Thirteen (50%) of the carcasses were scavenged by red foxes only and 2 (8%) by pine martens only. Three carcasses were not scavenged by either of the species. Eight carcasses were scavenged by both red foxes (N = 2 496 photos) and pine martens (N = 838 photos) but

the two species were never documented on the same photo. On 57 occasions (2%) at the 8 carcasses scavenged by both species, red foxes visited the carcasses after the pine martens had left (median 7 hours) and only on 8 (14%) occasions, within 1 hour (13-33 minutes). On 55 occasions (7%) pine martens visited the carcass after the red foxes (median 4 hours) and 14 (25%) of these occasions were within 1 hour (3-57 minutes). The time of visit by red fox and pine marten after a visit by the other species did not differ significantly (Mann Whitney U-test, U = 3.26, p = 0.071).

Pine martens visited carcasses on average once per day during January to April but rarely visited carcasses during the rest of the year (excluding August and September when no carcasses were recorded). Red foxes showed the highest number of visits during spring (April to marten and red fox). Scavengers were recorded by movement-triggered May, average 5 visits/day), an intermediate number (on average 1 visit/day) during winter (October to March), and few visits during summer (June to July, Fig. 1). The daily activity pattern differed significantly between pine martens and red foxes among the 6 time periods (X^2_5 = 124.153, P <0.001). Pine marten showed the highest activity between 20:00 and 24:00 (32% of all visits) whereas the red fox had the highest activity between 00:00 and 04:00 (30% of all visits). Although the two species demonstrated a significantly different temporal pattern of the visits made to carcasses there was a positive overall correlation in the timing of visits, i.e. how these four-hour periods were ranked from highest to lowest activity (Spearman rank correlation, N = 6, Rho = 0.886, P = 0.048, Fig. 2).

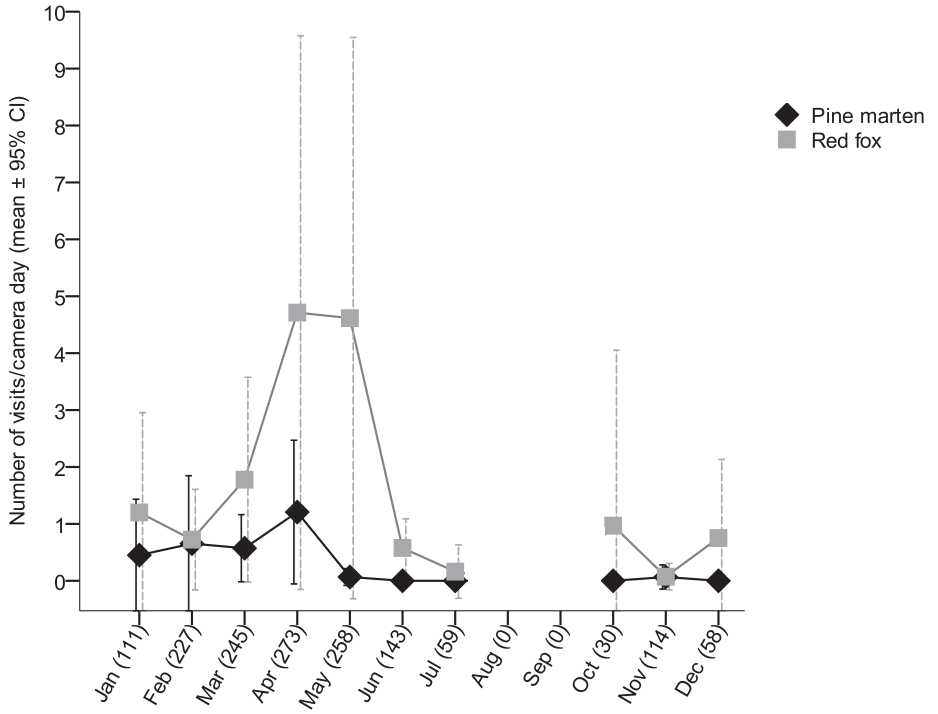

Figure 1. Average number of visits to wolf-killed moose sites (N = 23) per camera day in relation to month (n-value is shown in parenthesis) and scavenging species (pine marten and red fox). Scavengers were recorded by movement-triggered cameras during October to July in south-central Sweden, 2007-2009.

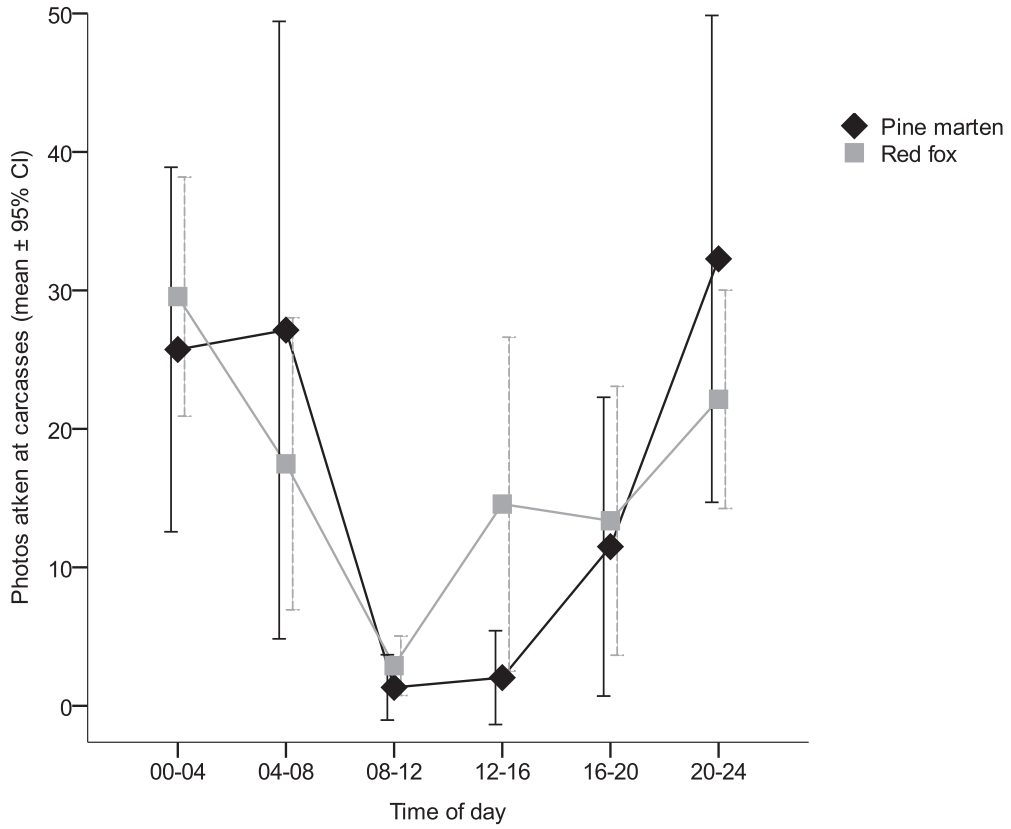

Figure 2. Daily scavenging pattern by pine marten (*N* = 850, 10 carcasses) and red fox (*N* = 3982, 21 carcasses) per wolf-killed moose. Scavengers were recorded by movement-triggered cameras in south-central Sweden, 2007-2009.

Patch use - The type of habitat at carcass sites (*N* = 26) significantly affected the presence of pine martens as there was a higher proportion of visits to carcasses in forests 21-60 years of age (70%, *N* = 10) compared to forests 0-20 years of age (15%, *N* = 13) and forests >60 years old (33%, *N* = 3; Table 1). The presence of red foxes at carcasses did not affect the presence of pine martens (Table 1) nor was the number of visits by red foxes significantly related to the number of visits by pine martens (*N* = 26, F = 0.662, R^2 = 0.027, *P* = 0.424). In contrast to pine martens, the presence of red foxes at carcasses was not affected by the type of habitat (Table 1).

Behaviour when feeding - Behaviour at wolf-killed carcasses differed significantly between red foxes and pine martens with martens being more vigilant (32% of the photos) than red foxes (22%), and feeding less (56%) than red foxes (68%), while other types of behaviour were of similar frequency, pine marten (12%) and red fox (10%, X^2_2 = 50.826, *P* <0.001, Fig. 3a). On 99 (36%) out of 275 occasions where pine martens showed vigilant behaviour they were standing on their hind legs, thus further increasing their area of observation. The sample size did not

allow for further comparisons of vigilance at carcasses that were only visited by pine martens and those visited by both species.

Vigilant behaviour was not caused by the presence of the cameras as pine martens looked in the direction of the camera in 33 (12%) out of 275 occasions which is less than expected (69 out of 275, $X^2_1 = 15.599$, $P < 0.001$). However, the red fox looked in the direction of the camera in 297 (34%) out of 886 occasions, which is more often than expected (222 out of 886, $X^2_1 = 15.327$, $P < 0.001$).

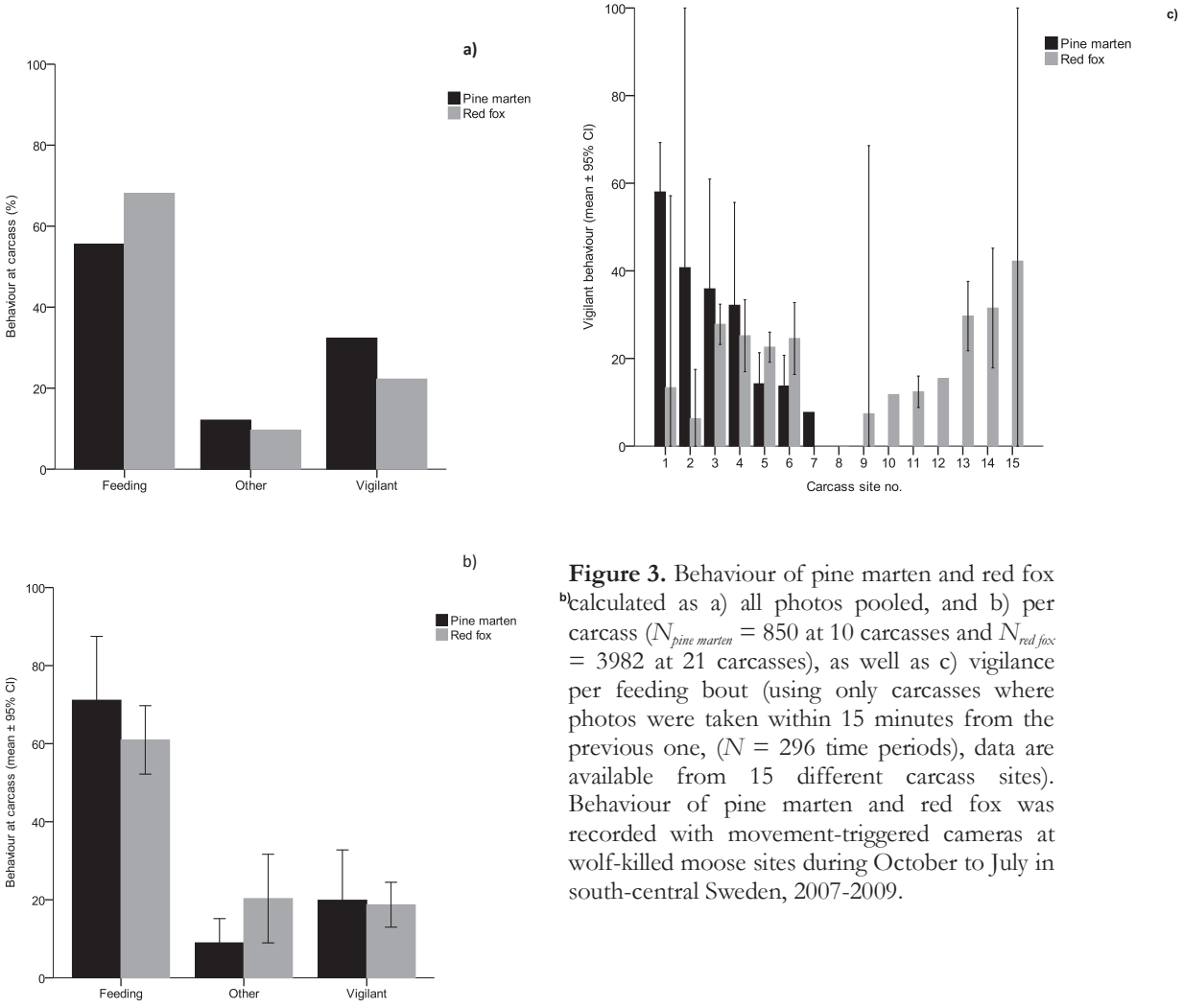

Figure 3. Behaviour of pine marten and red fox calculated as a) all photos pooled, and b) per carcass ($N_{pine\ marten}$ = 850 at 10 carcasses and $N_{red\ fox}$ = 3982 at 21 carcasses), as well as c) vigilance per feeding bout (using only carcasses where photos were taken within 15 minutes from the previous one, (N = 296 time periods), data are available from 15 different carcass sites). Behaviour of pine marten and red fox was recorded with movement-triggered cameras at wolf-killed moose sites during October to July in south-central Sweden, 2007-2009.

Table 1. Effects of habitat (forest age) and occurrence of red fox (only for pine marten) on the presence or absence of pine marten and red fox at remains after wolf-killed moose (N = 26), using logistic regression. Presence of pine marten and red fox at carcass sites were recorded with movement-triggered cameras in south-central Sweden, during October to July, 2007-2009.

Model	Explanatory variables	ß	SE	P	Exp (ß)	95% CI for ß	
	Parameter estimates					Lower	Upper
Pine marten	Forest age			**0.045**			
	60-120	1.065	1.482	0.472	2.899	0.159	52.910
	21-60	2.563	1.038	**0.014**	12.977	1.698	99.174
	0-20	0					
	Red fox	-0.217	1.250	0.862	0.085	0.070	9.323
Red fox	Forest age			0.984			
	60-120	19.999	23205.422	0.999	$4.84*10^{-8}$	0.000	-
	21-60	0.182	1.029	0.859	1.200	0.160	9.013
	0-20	0					

Thus, although less vigilant than the pine marten the behaviour of the red fox might have been biased by the presence of the camera. Therefore, we repeated the analyses of behaviour by excluding vigilant behaviour directed towards the camera for both species. To avoid bias from variation in the placement of the camera in relation to the carcass, we only used carcasses where both species were present for this analysis (N = 8, 3063 photos). For this subsample of observations, differences in behaviour between species were similar to the result based on the total dataset. Pine martens were more vigilant (30%) than red foxes (19%), they fed less (57%) than red foxes (72%), while other types of behaviour were almost equally frequent, pine marten (13%) and red fox (9%; $X^2_2 = 58.170$, $P < 0.001$). Inspection of data revealed that differences in vigilance between red foxes and pine martens were affected by carcass site (Fig. 3b and c). Vigilance by pine martens was not affected by red fox activity or by the time of day (Table 2) but was dependent on habitat, visibility and coverage at carcass sites (Table 3). Pine martens increased their vigilance by ~130% in habitats with high (open habitat) compared to low (dense habitat) visibility. The corresponding figure for high versus low coverage was ~88%. Vigilance by red foxes was not affected by habitat characteristics (Table 3).

Table 2. Effects of fox activity (number of visits) on the proportion of vigilant behaviour per time period (divided into 4-hours' time periods, *N* = 25) by pine marten at remains after wolf-killed moose (at carcasses visited by both species, *N* = 8), using linear mixed model. Behaviour of pine marten and red fox activity was recorded with movement-triggered cameras during October to July of 2007-2009.

Explanatory variables	ß	SE	P	95% CI for ß	
				Lower	Upper
*Intercep*t	0.585	0.130	<0.001	0.311	0.859
Fox activity	-0.000	0.000	0.331	-0.001	0.000
Time – 00-04	-0.087	0.053	0.115	-0.198	0.024
Time – 04-08	-0.068	0.065	0.309	-0.206	0.069
Time – 08-12	-0.139	0.121	0.266	-0.395	0.116
Time – 12-16	-0.033	0.087	0.708	-0.216	0.150
Time – 16-20	-0.072	0.066	0.291	-0.210	0.067
Time – 20-24	0				

Table 3. Effects of habitat, visibility and coverage on the proportion of vigilant behaviour per feeding bout by pine marten (*N* = 69) and red fox (N = 227) at remains after wolf-killed moose (*N* = 15), using linear mixed model. The behaviour was recorded with movement-triggered cameras during October to July of 2007-2009.

Model	Explanatory variables	ß	SE	P	95% CI for ß	
					Lower	Upper
Pine marten	*Intercep*t	0.894	0.295	0.004	0.305	1.483
	Forest age – 60-120	-0.583	0.211	**0.007**	-1.005	-0.162
	Forest age – 21-60	0.001	0.208	0.994	-0.415	0.418
	Forest age – 0-20	0				
	Visibility – dense	-0.293	0.113	**0.012**	-0.519	-0.068
	Visibility – open	0				
	Coverage – dense	-0.318	0.114	**0.007**	-0.545	-0.091
	Coverage – open	0				
Red fox	*Intercep*t	0.410	0.123	0.001	0.168	0.652
	Forest age – 60-120	-0.131	0.137	0.343	-0.401	0.140
	Forest age – 21-60	-0.026	0.150	0.861	-0.322	0.270
	Forest age – 0-20	0				
	Visibility – dense	0.109	0.106	0.302	-0.099	0.318
	Visibility – open	0				
	Coverage – dense	-0.011	0.152	0.943	-0.310	0.288
	Coverage – open	0				

DISCUSSION

Our study shows that red foxes visited a higher proportion of carcasses from wolf-killed moose and did so at a higher frequency than pine martens. This was most likely a result of the broader habitat use by the red fox compared to the more habitat-specialised pine marten, allowing red foxes to find and utilize a broader range of carcasses. However, this may also be related to the higher density of red fox compared to pine marten. Pine martens showed more vigilant behaviour than red foxes but had neither an overall different daily activity pattern than red foxes, nor were pine martens more vigilant during time periods of high activity by red foxes. Our study shows some support for the importance of interspecific predation risk leading smaller sized predators to trade-off foraging for increased vigilance. However, in our study habitat characteristics and visibility around feeding sites affected vigilance patterns more than the mere presence of a

potential competitor and larger sized predator. We do not know if the higher vigilance by pine martens in open areas were caused by the presence of red fox. Presence of other predators like lynx (*Lynx lynx*), golden eagle (*Aquila chrysaetos*) and other birds of prey may also affect the behaviour of pine martens.

Carcass availability in a scavenger home range is affected by habitat composition as carcasses in preferred habitats will be more frequently used than carcasses in non-preferred habitats (Jędrzejewski and Jędrzejewska 1992; Gese et al. 1996, Selva et al. 2005). If the best feeding habitat also is the most risky, animals must make a trade-off between feeding and vigilant behaviour (Lima and Dill 1990). The restricted habitat use previously shown for pine martens (Pedrini et al. 1995) was also confirmed in our study as the location of the carcasses obviously limited their use. This pattern was not shown by red foxes which exploit a wider range of habitats (Weber and Meia 1996) and were unaffected by visibility around carcasses. Nevertheless, in the preferred habitat for pine martens the habitat characteristics influenced their behaviour with more vigilant behaviour observed in open than in closed habitats. Pine martens are known to avoid open areas due to the increased predation risk in these habitats (Brainerd and Rolstad 2002; Rondinini and Boitani 2002) and our results showing increased vigilance in habitats with open compared to dense visibility confirm this pattern. None of our recorded carcasses was located in completely open terrain but the effect of visibility and coverage at carcass sites on the behaviour of pine martens was still obvious.

The almost similar daily activity pattern of carcass use shown by pine martens and red foxes did not support the idea of a crepuscular or diurnal activity pattern by pine martens to avoid red foxes. However, the daily peak of activity was in the early night for pine martens, whereas red fox activity peaked late at night. As pine martens were not proportionately more vigilant during time periods when red foxes were most active, this suggests that they may not perceive the increased risk of encounters with red foxes as requiring a major change in their feeding behaviour. In our study area, direct encounters with red foxes at carcasses where pine martens were present were probably very rare as visits by red foxes mostly occurred several hours after pine martens had left carcass sites. Also, there may be an interspecific transfer of information in sympatric carnivores as to the whereabouts of good feeding opportunities (Krebs and Dawkins 1984), as for example when foxes are reported to follow badgers to good foraging sites (Macdonald 1987). In this study, we once recorded a red fox and badger feeding together at the same carcass, but never red foxes and pine martens. However, in 25% of all their visits, the pine martens arrived at a carcass within 1 hour after the red fox had left which may indicate that the pine marten to some extent adopted a following strategy.

Animals commonly display different types of vigilance which might differ in intensity and in the costs associated, depending on whether feeding is interrupted or not (Lima and Bednekoff 1999). In dense habitats, vigilance is improved by an upright posture for smaller mammals (Sharpe and van Horne 1989). The display of overt vigilance, such as adopting an upright posture, might enable the animal to spot enemies at longer distances but could also serve as a signal to the predator deterring its attack (Scannell et al. 2001). Our study showed that pine

martens exhibited an upright posture during one third of their vigilant time, thus very likely making a trade-off between time devoted to overt vigilance and consumption as an anti-predator strategy. For red foxes, only one type of vigilant behaviour occurred according to the photos taken. The lower level of vigilance shown by red foxes may be a direct response to several generations of zero or negligible wolf presence in Scandinavia (Wabakken et al. 2001), albeit there has always been a predation risk from lynx and birds of prey. This may have caused red foxes to underestimate the predation risk from the re-establishing wolf population, as has also been shown in moose behaviour (Sand et al. 2006a).

At temperate latitudes such as in northern and central Europe, large herbivore carcasses are usually available for very long time periods during the cold season (Selva et al. 2003). In our study, red foxes and pine martens continued to use carcasses several months after the time of death, suggesting that scavenging on wolf-killed moose constitutes an important food resource for these species. This may be especially important during spring, which usually is a critical period for survival and growth of reproducing animals and their new-born offspring (Clutton-Brock 1988). In our study, pine martens utilized carcasses almost only during the late winter months (January to April) and did not rely on carcasses at all during the summer and early winter. Utilization of carcasses as an alternative food resource may relate to the abundance of the main prey of pine martens (such as rodents and birds) where for example the abundance of birds increase in May (Helldin 1999; 2000). Red foxes were highly active at carcasses in April and May, a pattern also supported by previous studies (Sidorovich et al. 2005; Selva et al. 2005), rarely scavenged during summer, and scavenged slightly less during the winter months than in April and May. The slightly earlier seasonal utilization period in scavenging by pine martens compared to red foxes in our study may reflect that the time of parturition for red foxes occurs slightly later in spring (April to May; Lindström 1981) than for pine martens (March to April; Zalewski 2001) which thus correlated with periods of activity peak at carcass sites. This suggests that the prime reason for the seasonal partitioning of scavenging may have more to do with reproductive timing and rearing of offspring than avoiding intra-guild predation. Large carnivore restoration may sometimes result in important ecosystem shifts by altering the quantity and timing of carrion available to scavengers (Wilmers et al. 2003). Whereas carcasses resulting from natural mortality depend on the season, wolf-killed ungulates provide a more constant and predictable food resource for scavengers over the year (Wilmers et al. 2003; Selva and Fortuna 2007). This pattern is also shown in our study area where presence of wolves reduced the seasonal variation of biomass from moose carcasses and most important, increased it during spring (Wikenros et al. 2013). Consequently, the steadily growing Scandinavian wolf population will likely benefit both the red fox and pine marten populations through increased food supply during certain/critical times of the year.

Acknowledgments

We thank P. Ahlqvist who conducted parts of the field work. We are grateful to A. Angerbjörn and P. Kjellander who provided constructive comments on an earlier version of the manuscript. The study was funded by the Swedish Research Council for Environment, Agricultural Sciences and Spatial Planning (FORMAS), the

Swedish Environmental Protection Agency, the Swedish Association of Hunting andWildlife Management, World Wildlife Fund for Nature (WWF-Sweden), the Swedish University for Agricultural Sciences (SLU), the Olle and Signhild Engkvist Foundations, the Carl Trygger Foundation, the Axel and Margaret Ax:on Johnson Foundation, the Helge Ax:on Johnsons Foundation, and the Swedish Carnivore Association.

Literature Cited

ATWOOD, T. C., AND E. M. GESE. 2008. Coyotes and recolonising wolves: social rank mediates risk-conditional behaviour at ungulate carcasses. Animal Behaviour 75: 753–762.

BRAINERD, S. M., AND J. ROLSTAD. 2002. Habitat selection by Eurasian pine martens *Martes martes* in managed forests of southern boreal Scandinavia. Wildlife Biology 8: 289–297.

BUSKIRK, S. W., AND L. F. RUGGIERO. 1994. American marten. Pp. 7-37 in The scientific basis for conserving forest carnivores: American marten, fisher, lynx, and wolverine in the western United States (L. F. Ruggiero, K. B. Aubrey, S. W. Buskirk, L. J. Lyon, and W. J. Zielinski, eds.). United States Forest Service General Technical Report, RM-254.

CARO, T. M. 1987. Cheetah mothers' vigilance: looking out for prey or for predators. Behavioral Ecology and Sociobiology 20: 351–361.

CARO, T. M., AND C. J. STONER. 2003. The potential for interspecific competition among African carnivores. Biological Conservation 110: 67–75.

CLUTTON-BROCK, T. H. 1988. Reproductive success. Pp 472-485 in Reproductive Success (T. H. Clutton-Brock, ed.). The University of Chicago Press, Chicago, USA.

COZZI, G., F. BROEKHUIS, J. W. MCNUTT, L. A. TURNBULL, D. W. MACDONALD, AND B. SCHMID. 2012. Fear of the dark or dinner by moonlight? Reduced temporal partitioning among Africa's large carnivores. Ecology 93: 2590–2599.

CUTLER, T. L., AND D. E. SWANN. 1999. Using remote photography in wildlife ecology: a review. Wildlife Society Bulletin 27: 571–581.

DAHLSTRÖM, B. 1995. Snötäcke. Pp 91-97 in Klimat, sjöar och vattendrag (B. Raab, and H. Vedin, eds). Gävle, Sweden: Kartförlaget. (In Swedish.)

GESE, E. M., R. L. RUFF, AND R. L. CRABTREE. 1996. Foraging ecology of coyotes (*Canis latrans*): the influence of extrinsic factors and a dominance hierarchy. Canadian Journal of Zoology 74: 769–783.

GUTHRIE, C. G., AND D. L. MOORHEAD. 2002. Density-dependent habitat selection: evaluating isoleg theory with a Lotka-Volterra model. Oikos 97: 184–194.

HARRINGTON, L. A., ET AL. 2009. The impact of native competitors on an alien invasive: temporal niche shifts to avoid interspecific aggression? Ecology 90:1207–1216.

HELLDIN, J.-O. 1999. Diet, body condition, and reproduction of Eurasian pine martens *Martes martes* during cycles in microtine density. Ecography 22: 324–336.

HELLDIN, J.-O. 2000. Seasonal diet of pine marten (Martes martes) in southern boreal Sweden. Acta Theriologica 45: 409–420. 00.

JĘDRZEJEWSKI, W., AND B. JĘDRZEJEWSKA. 1992. Foraging and diet of the red fox *Vulpes vulpes* in relation to variable food resources in Białowieża National Park, Poland. Ecography 15: 212–220.

KIMBRELL, T., R. D. HOLT, AND P. LUNDBERG. 2007. The influence of vigilance on intraguild predation. Journal of Theoretical Biology 249: 218–234.

KOEHLER, G. H., AND M. G. HORNOCKER. 1977. Fire effects on marten habitat in the Selway-Bitteroot Wilderness. The Journal of Wildlife Management 4: 500–505.

KREBS, J. R., AND R. DAWKINS. 1984. Animal signals: mind-reading and manipulation. Pp 380-405 in Behavioural ecology. (J. R. Krebs, and N. B. Davies, eds.). Blackwell Scientific, Oxford, UK.

LANSZKI, J., A. ZALEWSKI, AND G. HORVATH. 2007. Comparison of red fox *Vulpes vulpes* and pine marten *Martes martes* food habits in a deciduous forest in Hungary. Wildlife Biology 13: 258–271.

LIMA, S. L., AND B. A. BEDNEKOFF. 1999. Back to the basic of anitpredatory vigilance: can nonvigilant animals detect attack? Animal Behaviour 58: 537–543.

LIMA, S. L., AND L. M. DILL. 1990. Behavioural decisions made under the risk of predation: a review and prospectus. Canadian Journal of Zoology 68: 619–640.

LINDSTRÖM, E. 1981. Reliability of placental scar counts in the Red fox (*Vulpes vulpes* L.) with special reference to fading of the scars. Mammal Review 11: 137–149.

LINDSTRÖM, E. R. 1989. The role of medium-sized carnivores in the Nordic boreal forest. Finnish Game Research 46:53–63.

LINDSTRÖM, E. R. 1991. Pattern of spread and effects of sarcoptic mange among red fox populations in Sweden. Pp 591-595 in Global trends in wildlife management (B. Bobek, K. Perzanowski, and W. Reglin, eds.). Trans. 18th IUGB Congress, Kraków 1987. Świat-Press, Kraków, Warsawa, Poland.

LINDSTRÖM, E. R., S. M. BRAINERD., J. O. HELLDIN, AND K. OVERSKAUG. 1995. Pine marten - red fox interactions: a case of intraguild predation? Annales Zoologici Fennici 32: 123–130.

MACDONALD, D. W. 1987. Running with the fox. Unwin Hyman, London, UK.

PALOMARES, F., AND T. M. CARO. 1999. Interspecific killing among mammalian carnivores. American Naturalist 153: 492–508.

PIANKA, E. R. 1969. Habitat specificity, speciation, and species density in Australian desert lizards. Ecology 50: 498–502.

PIANKA E. R. 1974. Niche Overlap and Diffuse Competition. Proceedings of the National Academy of Sciences of the United States of America 71: 2141–2145.

RASA, O. A. E. 1989. The cost and effectiveness of vigilance behavior in the dwarf mongoose: implications for fitness and optimal group size. Etholoy Ecology and Evolution 1: 264–282.

RICKLEFS, R. E., ET AL. 1990. Biotic systems and diversity. Pp 159-168 in Report of working group 4, Interlaken workshop for past global changes. Global and Planetary Change 82.

RITCHIE, E. G., AND C. N. JOHNSON. 2009. Predator interactions, mesopredator release and biodiversity conservation. Ecology Letters 12: 982–998.

RONDININI, C., AND L. BOITANI. 2002. Habitat use by beech martens in a fragmented landscape. Ecography 25: 257–264.

ROSENZWEIG, M. L. 1981. A theory of habitat selection. Ecology 62: 327–335.

SAND, H., P. WABAKKEN, B. ZIMMERMAN, Ö. JOHANSSON, H. C. PEDERSEN, AND O. LIBERG. 2008. Summer kill rates and predation pattern in a wolf-moose system: can we rely on winter estimates? Oecologia 156: 53–64.

SAND, H., C. WIKENROS, P. WABAKKEN, AND O. LIBERG. 2006a. Cross-continental differences in patterns of predation: will naive moose in Scandinavia ever learn? Proceedings of the Royal Society B 273: 1421–1427.

SAND, H., C. WIKENROS, P. WABAKKEN, AND O. LIBERG. 2006b. Wolf (*Canis lupus*) hunting success on moose (*Alces alces*): effects of hunting group size, snow depth and age of breeding wolves. Animal Behaviour 72: 781–789

SAND, H., B. ZIMMERMAN, P. WABAKKEN, H. ANDRÉN, AND H. C. PEDERSEN. 2005. Using GPS-technology and GIS-cluster analyses to estimate kill rates in wolf-ungulate ecosystems. Wildlife Society Bulletin 33: 914–925.

SCANNELL, J., G. ROBERTS, AND J. LAZARUS. 2001. Prey scan at random to evade observant predators. Proceedings of the Royal Society B 268: 541–547.

SELVA, N., B. JĘDRZEJEWSKA, W. JĘDRZEJEWSKI, AND A. WAJRAK. 2003. Scavenging on European bison carcasses in Bialowieza Primeval Forest (eastern Poland). Ecoscience 10: 303–311.

SELVA, N., B. JĘDRZEJEWSKA, W. JĘDRZEJEWSKI, AND A. WAJRAK. 2005. Factors affecting carcass use by a guild of scavengers in European temperate woodland. Canadian Journal of Zoology 83: 1590–1601.

SELVA, N., AND M. A. FORTUNA. 2007. The nested structure of a scavenger community. Proceedings of the Royal Society B 274: 1101–1108.

SHARPE, P. B., AND B. VAN HORNE. 1998. Influence of habitat on behavior of Townsend's Ground Squirrels (*Spermophilus townsendii*). Journal of Mammalogy 79: 906–918.

STORCH, I., LINDSTRÖM, E., AND J. DE JOUNGE. 1990. Habitat selection and food habitatsof the pine marten in relation to competition with the red fox. Acta Theriologica 35:311–320.

SWANN, D. E., C. C. HASS, D. C. DALTON, AND S. A. WOLF. 2004. Infrared-triggered cameras for detecting wildlife: an evaluation and review. Wildlife Society Bulletin 32: 357–365.

SCHOENER, T. W. 1986. Mechanistic approaches to community ecology - a new reductionism. American Zoologist 26: 81–106.

SIDOROVICH, V. E., D. A. KRASKO, AND A. A. DYMAN. 2005. Landscape-related differences in diet, food supply and distribution pattern of the pine marten, Martes martes in the transitional mixed forest of northern Belarus. Folia Zoologica 54: 39–52.

STORCH, I., E. LINDSTRÖM, AND J. DE JOUNGE. 1990. Habitat selection and food habits of the pine marten in relation to competition with the red fox. Acta Theriologica 35: 311–320.

SWEDISH ASSOCIATION FOR HUNTING AND WILDLIFE MANAGEMENT. 2010. http://www.jagareforbundet.se/Viltet/ViltVetande/Artpresentationer

VEDIN, H. 1995 Lufttemperatur. Pp 44-57 in Klimat, sjöar och vattendrag (B. Raab, and H.

Vedin, eds). Gävle, Sweden: Kartförlaget. (In Swedish.)

VIRGÒS, E., ZALEWSKI, A., ROSALINO, L. M., AND M. MERGEY. 2012. Habitat ecology of *Martes* species in Europe: a review of the evidence. Pp 255-266 in Biology and conservation of martens, sables, and fishers. a new synthesis. (K. B. Aubry, W. J. Zielinski, M. G. Raphael, G. Proulx, and S. W. Buskirk eds.). Cornell University Press, Ithaca and London.

WABAKKEN, P., H. SAND, O. LIBERG, AND A. BJÄRVALL. 2001. The recovery, distribution, and population dynamics of wolves on the Scandinavian peninsula, 1978-1998. Canadian Journal of Zoology 79: 710–725.

WABAKKEN, P., ET AL. 2009. The wolf in Scandinavia: status report of the 2008–2009 winter. Oppdragsrapport no. 6–2009. Høgskolen i Hedmark, Elverum, Norway.

WATTS, H. E., AND K. E. HOLEKAMP. 2008. Interspecific competition influences reproduction in spotted hyenas. Journal of Zoology 276: 402–410.

WHITE, P. C. L., SAUNDERS, G. AND HARRIS, S. 1996. Spatial-temporal patterns of home range use by foxes (*Vulpes vulpes*) in urban environments. Journal of Animal Ecology 65: 121–125.

WEBER, J. M., AND J. S. MEIA. 1996. Habitat use by the red fox *Vulpes vulpe*s in a mountainous area. Ethology Ecology and Evolution 8: 223–232.

WIKENROS, C., SAND, H., AHLQVIST, P., AND O. LIBERG. 2013. Biomass flow and scavengers use of carcasses after re-colonization of an apex predator. PLOS ONE 8 (10) e77373.

WILMERS, C. C., R. L. CRABTREE, D. W. SMITH, K. M. MURPHY, AND W. M. GETZ. 2003. Trophic facilitation by introduced top predators: grey wolf subsidies to scavengers in Yellowstone National Park. Journal of Animal Ecology 72: 909–916.

ZALEWSKI, A. 2001. Seasonal and sexual variation in diet activity rhythms of pine marten *Martes martes* in the Białowieża National Park (Poland). Acta Theriologica 46: 295–304.

ZALEWSKI, A., AND W. JĘDRZEJEWSKI. 2006. Spatial organisation and dynamics of the pine marten *Martes martes* population in Białowieża Forest (E Poland) compared with other European woodlands. Ecography 29: 31–43.

PAPER II

Quantifying prey selection of northern and southern European wolves *(Canis lupus):* Scandinavia and Tuscany

SOPHIE STÅHLBERG, ELENA BASSI, VIVIANA VIVIANI AND MARCO APOLLONIO

Department of Natural and Environmental Science, University of Sassari, Via Muroni 25, Sassari 07100, Sassari, Italy.

Abstract

Wolf diet is determined by several ecological factors which differ with latitude and human impact. European wolves differ somewhat in size and latitude affects prey alternative and the human impact on the diet composition. Scats were collected and analysed for nine years in south-central Scandinavia and four years in Tuscany, Italy, where habitat heterogeneity and prey density was compared in different ecological perspectives. Climate differences has several effects on prey choice during summer and winter, but also higher effect on prey age in colder regions as was shown in south-central Scandinavia. Diet composition in Scandinavia showed a stable and negligible variance while Tuscany varied noticeably through the years. This is most likely related to the fact that heavy forestry industry in Scandinavia restricts biodiversity while abandoned agricultural landscape with re-forestation in the Apennines has positively changed wolf habitat heterogeneity resulting in higher variation in prey choice and prey abundance. The risk of injury from prey was shown to be more important for the Tuscan wolves and depredation on domestic animals was higher due to higher human density, but the reason for this may well be the different approaches of animal husbandry, not prey abundance and density.

Key words: *Canis lupus*, diet composition, scat analysis, prey density, prey age class, prey variation, biomass, habitat heterogeneity

Introduction

An animal exhibits a preference for a particular type of food when the proportion of that type in the animal's diet is higher than its proportion in the environment (MacArthur and Pianka 1966). Ranked preferences are usually seen most clearly amongst carnivores who actively select prey items that are the most profitable in terms of energy intake per unit time spent handling prey, i.e. the "functional response", classified by Holling (1959a, b). Wolves are highly adaptive and behaviourally flexible carnivores that have evolved to hunt prey widely ranging in size, although they are most commonly categorised as cursorily hunters of large ungulates (Peterson and Ciucci 2003).

Wolves are most often territorial and hunt within their home range where the prey species are determined by the habitat resources and threats. When wild prey species are limited or scarce, they are opportunistic and have the ability to utilise other food sources such as domestic animals, garbage, carcasses, marine species and vegetation (Salvador and Abad 1987; Okarma 1995; Darimont et al 2003; Stahler et al 2006; Watts et al 2010). Moreover wolves can both scavenge and predate, and they switch between the two strategies depending on what is most profitable (Stephens & Krebs 1986). Furthermore, it is obvious that when the environmental characteristics change, the relation between wolves and preys changes as well. During the past decades, many studies have been carried out to define wolves food habits in different areas, and one common result is that ungulates are the main preys within its range (Sand et al 2005; Meriggi et al 2011); moreover nearly all ungulates species are used by wolves within their range, and it seems that in each local area wolf became very skilled on hunting a specific one (Sand et al 2012). Extensive information regarding the feeding ecology of wolves using scat analysis have been done in Italy (Mattioli et al 1995 and 2011; Capitani et al 2004; Gazzola et al 2007; Meriggi et al 2011;

Milanesi et al 2012) but very few in SCA, e.g. the on-going Scandinavian Wolf Research Project (http://skandulv.nina.no; Olsson et al 1997).
In this study, we used scat analysis for determining prey selection in two different European areas: one in northern Europe, located in Scandinavia, mainly south-central Sweden, and the other one located in Tuscany, north-central Italy. The objective of this study is to compare the wolf diets in the two areas which show clear differences both in climate (i.e. colder and longest winter in Scandinavia) and in human density (i.e. higher density in Italy). We tested the hypothesis that habitat features determine the outcome of the wolf diet in the different areas and predicted that 1) the prey species with the highest density is selected by wolves, 2) as Italian wolves weigh 20% less than Swedish wolves, they should feed on smaller prey species, 3) Scandinavian wolves selects juvenile moose more than Tuscan wolves selects cervid fawns due to the size relation, and 4) higher human density in Italy will result in a higher proportion of domestic animals in the diet than in Scandinavia.

Material and methods

Study areas

Fig 1. Wolf diet analysis in south-central SCA and TUS, Italy.

South-central Scandinavia
Grey wolves were functionally extinct from the Scandinavian, peninsula by late 1960s (Haglund 1968) but by the late 1970s, wolves reappeared and there has been successful reproductions all years but 1986 (Wabakken et al 2001) and the recolonizing wolf population counts 252-291 individuals (Wabakken et al 2010). Major part of the population is located in south-central Sweden where wolves have been protected since 1966 until 2010.

Data collected in south-central Scandinavia, hereafter abbreviated SCA, 59º-61ºN, 12º-17ºE, from 1997 to 2006 in 18 wolf territories in Sweden, located in the counties Värmland, Dalarna, Örebro, Västra Götaland and two in Norway, Våler and Römskog; (1) Leksand, (2) Hasselfors, (3) Grangärde, (4) Nyskoga, (5) Hagfors, (6) Tyngsjö, (7) Tisjön, (8) Furudal, (9) Dals-Ed, (10) Koppang, (11) Filipstad, (12) Årjäng, (13) Bograngen, (14) Glaskogen, (15) Uttersberg, (16) Malung, (17) Atndalen, (18) Gravendal, (19) Römskog N, (20) Våler N. Altitude ranging from 50 to 1000 m.a.s.l. and the total study area was 17,370 km².
Boreal temperate forest in the cold temperate climate zone with snow cover 3-6 months/year and varying snow depths of 10-75 cm. Coniferous forest (taiga) is the dominant vegetation type and locally in the mountains also tundra is present. . The limit to the tundra coincides basically with the tree line which is nearly 900 m altitude in the southern mountains. The climate is continental with temperatures ranging from 15°C in July and –7°C in January. Precipitation in 2000-2005 was 600-1200 mm/year (Swedish Meteorological and Hydrological Institute). SCA's boreal forests (300 000 km² in Norway and Sweden) are among the most intensively exploited forests in the world, with less than 5% virgin forest left standing. Naturally reseeded or replanted stands are clear-cut on a 70–80 year cycle using a highly mechanised system and a dense network of forest roads (Linell et al 1999). The vegetation is dominated by coniferous forests of Scots pine *(Pinus sylvestris)* and Norway spruce *(Picea abies)*. Common deciduous species included birch *(Betula pubescens)*, willow *(Salix* spp), aspen (*Populus tremula*), and alder (*Alnus incana, A. glutinosa*). Moose *(Alces alces)* and roe deer

(Capreolus capreolus) are the main prey species (Sand et al 2005, 2008) and other prey species available included are beaver (*Castor fiber*), mountain hare (*Lepus timidus*), capercaillie (*Tetrao urogallus*), and black grouse (*Tetrao tetrix*). Other large or medium-sized mammalian predators present in wolf territories are brown bear *(Ursus arctos)*, Eurasian lynx *(Lynx lynx)*, red fox *(Vulpes vulpes)* and, in a few, wolverine *(Gulo gulo)*. Human hunting of wild ungulates is a very widespread, but carefully regulated, activity (Cederlund and Bergström 1996). Wolves >24 months mean weight is 40.7 kg (females 36.9 kg, males 44.5 kg) in Sweden (National Veterinary Institute). Human population density in Sweden is 20/km², but in the study area the density is less than 1/km²(Swedish National Atlas 1991). Due to extensive logging, the study areas are easily accessible to humans by a network of gravel forest roads (0.62 km/ km²) (Eriksen et al 2009).

Tuscany, Italy

The estimated wolf population size in Italy is approximately thousand individuals, even though exact numbers are lacking, it has increased in recent years (Boitani 2003). Tuscany, hereafter abbreviated TUS, is located in north-central Italy and is a probable source of dispersing wolves to the Alps (Scandura et al. 2001; Fabbri et al 2007). Wolf habitat status differs geographically and three areas with wolf territories were examined in TUS. Previous studies have been carried out in the Tuscan provinces which we are taking into consideration; in Arezzo, Casentinesi Forests next to Alpe di Catenaia (Mattioli et al. 1995, 2004, 2011, Apollonio et al 2004), in Lucca, the Orecchiella area (Ciucci et al 1996) and in Pisa, the Val di Cecina area (Capitani et al 2004). The three study areas in TUS are Alpe di Catenaia in Arezzo Province, Orecchiella in Lucca Province and Berignone in Pisa Province. We estimated one or two packs in each area. Main threats restricting survival and reproduction success are poaching, poisoning and traffic collisions according to provincial records. Average weigh for adult wolves in the study areas is 31.7 kg (females 27.1 kg, males 34.7 kg) in TUS (Arezzo Provincial Veterinary Department). Tuscan study areas were quite different: therefore their description is provided separately:

Alpe di Catenaia (43-48°N, 11-43°E). Data collected 2008-2009. Altitude 490-1400 m.a.s.l. The study area is 120 km² and includes a small protected area of 27 km² in the centre. The climate is continental and is characterized by high humidity and rainfall. Temperatures drop below freezing in winter with heavy snowfall occurring. Mean temperature 11.6 ° C (summer 17.5° C and winter 8° C). There is more than 80% forest cover with coppice, high trunk forests of Turkey oak (*Quercus cerris*) and chestnut (*Casanea sativa*) at lower elevation, and of beech (*Fagus sylvatica*) at upper ranges. Moreover conifers such as pine and black pine *(Pinus negra)*, white spruce *(Abies alba)*, Douglas fir *(Pseudotsuga spp)* are interspersed into deciduous woods or form small patches of pure forests. Prey species are wild boar *(Sus scrofa)* and roe deer. Sheep and goats are present in open areas throughout the year. Some large herds of cattle and horses are present in small number and close to farms and villages.

Orecchiella (44-11°N, 10-23°E). Data collected 2005-2006. The study area, Orecchiella Natural Park, is 52 km² and located in High Apennines, with altitudes ranging from 900 to 2054 m.a.s.l. It is included in a temperate cold climate zone, characterized by high rainfall mainly concentrated in autumn and spring. Summer rains are extensive, although irregular by the influence of the Mediterranean climate. The snowfalls are quite frequent and abundant in the medium-high park, especially in first three months of the year. In winter, the violence of the winds is especially felt on the ridge and in its vicinity, affecting the biotic communities. The forest landscape is dominated in the high forest of conifers and beech. At lower altitudes, it is possible to find Turkey oak *(Quercus cerris)* and chestnut *(Castanea sativa)*. Other species of trees and shrubs are: ash *(Fraxinus excelsior)*, laburnum *(Laburnum anagyroides)*, blackthorn *(Prunus spinosa)*, the mountain ash *(Sorbus air)* and the rowan tree *(Sorbus aucuparia)*. Prey species are mouflon *(Ovis orientalis musimon)*, red deer (*Cervus elaphus)*, roe deer, and wild boar.

Berignone -Val di Cecina - (43-20°N, 10-57°E). Data collected 2008-2009. Altitude 100-600 m.a.s.l. close to the Tyrrhenian coast. The study area covers 724 km². The Val di Cecina can be

considered a transition zone between the two major climatic regions in which Italy is divided: 1) Mediterranean climate with temperatures averages between 14 and 18 ° C and precipitation ranging between 300 and 900 mm/year with summer drought, 2) Central European climate with average temperatures between 9 and 13 ° C and rainfall between 420 and 1500 mm, with no dry period summer time, rarely snowfall. Wooded hills composed of deciduous and evergreen oak forests of *Quercus pubescence, Q. robur* and *Q. ilex*. Prey species are wild boar, fallow deer (*Dama dama*), roe deer, mouflon and small mammals. Sheep and goats are present in open areas throughout the year. Some large herds of cattle and horses are present in small number and close to farms and villages.

The only other mammalian predator in TUS is the red fox. Human density for the 3 Tuscan provinces are 107/km², 210/km², and 161/km² respectively for Arezzo, Lucca, and Pisa, but the actual inhabitants inside the study areas are <0,5/ km². Mean road densities inside the study areas are <1.5 km/km². The three study areas can be included in an area of about 8 000 km². Wolf main ungulate prey species in the Northern Apennines, wild boar and roe deer, has increased significantly between 1977-2004 (Meriggi et al 2011).

Sampling design for scat collection

Scats were collected along systematic transects in re-sealable plastic bags and frozen until laboratory analysis. They were identified in the field as most likely corresponding to wolves based on size (diameter >2.5 cm), shape and the presence of mammal prey remains such as hair, bones, claws and hooves or feathers.

Laboratory analysis

In SCA, the scats were frozen and prior to the analyses the scats were dried for 48h at 90°C (±5°C). After the drying process, dry weight of the scats was taken (0.01g precision). The procedure to analyse the scat contents followed Spaulding et al. (1997). Each scat was broken apart by hand and the single prey items were sorted. If there was more than one prey item found in the scat, we assumed that the macro and micro components originated from the found items in the same proportion (Ciucci et al 1996). We identified the macro components in the scats (e.g. bird remains, hairs, hooves, teeth) with the help of reference manuals (Moore et al 1974, Debrot et al 1982, Teerink 1991) and a reference collection developed at the Grimsö Research Station. The hairs were first examined visually concerning colour pattern, length, thickness, and thereafter identified microscopically by medullary pattern and cuticular scale (Teerink 1991). With the help of a reference grid we visually estimated the relative volumetric proportion for each prey item identified in a scat (Reynolds & Aebischer 1991). The distinction into juvenile and adult cervids was carried out due to the characteristic hair pattern of young animals. We were not able to distinguish consistently between juvenile and adult animals because the typical juvenile hair pattern is only visible from birth to the first autumn moult in August/September. Because of that, it is not possible to distinguish between juveniles and adults during the winter season by looking at the hairs (Peterson et al. 1984, Ciucci et al. 1996). To make a reasonable differentiation into juveniles and adults we applied the age class distribution for consumed cervids described by Pedersen et al (2005) according to: moose, adults:yearlings:calf = 80:10:10 and roe deer, fawns:adults = 50:50.

In Italy, the scats were kept dry and frozen at -30°C, scat were washed in a sieve of 0.5 mm and the prey remains (hairs and bones), fruit and grasses found in every scat were dried at 68°C for 24 h. Prey remains were identified through comparison to a reference collection of mammal hair, bones, and teeth. We identified the prey species and age or weight class (for ungulates only) when possible. This identification was based on the macroscopic characteristics of hairs and bones following Mattioli et al. (2004, and 2011). Wild boar remains were divided into three weight classes: newborn piglet (<10 kg), piglet (10–35 kg), and adult (>35 kg). Cervid remains were classified into two classes according to the first moult at 6 months of age: fawn (<7 months) and adult (≥7 months), equivalent to the SCA classification. In order to estimate the contribution of each species in the diet, in terms of volume, we categorized each food item in a scat by 5% steps (i.e. <5%; 6–10%; 11–15%) as described by Russell and Storch (2004). We

calculated the average volume (AV%) for each food item. The AV% was defined as $V_i/N \times 100$ where V_i is the total volume of a given food item i, and N is the total number of scats.

Prior to the analyses the observers were trained in identifying scat contents by practicing with reference material and reference scats. As recommended by Ciucci et al (1996), a blind test was performed with 30 scat samples to assess the accuracy of identification by the laboratory personal in both SCA and Italy. The errors were below the threshold of 5% (Mattioli et al 2004). For the analysis the year was divided in two seasons, according to the wolf biology: summer, and winter. As SCA has earlier winter and later summer periods than Italy, summer is considered as one month shorter in SCA. Thus summer is between the 1st of May and the 30th of September in SCA, and from the 1st of May to the 30th of October in Italy; while winter is between the 1st of October and the 30th of April in SCA, and from the 1st of November to the 30th of April in Italy.

Estimated biomass in scats

To estimate the biomass intake, we used the Whole Scat Equivalents (WSE), which summarises the relative dry volume for a given food item within the scat sample (Angerbjörn et al. 1999), for the SCAn data and the AV% for the Italian data. Yearly biomass ingested from the food items were estimated on the basis of the known relationship between prey biomass consumed per collectable scat produced, using three calculations; Floyd et al 1978, Weaver 1993 and Rühe et al 2003 (Table 2). Calculations are presented with the Floyd equation: $y = 0.383 + 0.02x$, Weaver equation: $y = 0.439 + 0.008x$ and Rüehe equation $y = 0.731 + 0.00406x$, where the x = assumed live weight of prey species and y = estimated biomass consumed per scat. For seasonal biomass calculation, we used the Weaver equation since neither Floyd nor Rüehe have been based on large ungulates such as moose (Table 4 and 5). Assumed live weights of prey species were gathered from previous studies (Feldhamer et al 1988; McElligott et al 2001; Santiago-Moreno et al 2005; Mitchell et al 1976; Olsson et al 1997; Sand et al. 2008) and adjusted according to prey type consumption, i.e. juvenile: adult relation.

Prey preference

Manly's preference index, α_i is a useful measure for quantifying predator preference in selective predation as it includes a random number of prey types of both constant and changing prey densities. To investigate prey preference, Manly's Alpha preference index, also known as Chesson's index (Chesson 1978) was used: $\alpha_i = (r_i/n_i) * [1/\Sigma(r_j/n_j)]$ where prey type r_i or r_j is the proportion in the diet and n_i or n_j the proportion in the environment. Manly's alpha ranges from 0 to 1; r_i and r_j are the proportions (biomass) of prey type *i* or *j* in the wolf diet, n_i and n_j are the proportions (biomass) of prey type *i* or *j* in the environment. Unselective predation occurs if $\alpha_i = 1/m$ (m = total number of prey types). Prey species *i* is preferred if α_i is greater than $1/m$, whereas negative selection is found if α_i is less than $1/m$. Conversely, if $\alpha_i = 1/m$, less of prey type *i* occurs than expected by random feeding, i.e. prey type *i* is avoided by the predator.

Niche width

The calculations of niche width were based on seven prey groups in SCA and eight in Italy. Levin's Food Niche Breadth (FNB) index (Levins 1968) was used to measure specialisation quantitatively for the wolf diet composition within SCA and TUS as well as between the countries. Levin's index is defined as $B = 1/\Sigma p_j^2$ where p_j = proportion of fractions of items in the diet that are of food category *j*. Levin's Food Niche Breadth can be standardised and expressed in a scale from 0 to 1 with the help of an equation, $B_A = (B-1)/(n-1)$ where B_A = Levin's standardised FNB, n = number of possible resource states.

Niche overlap

The calculations of niche overlap were based on seven in SCA and eight prey groups in TUS. To calculate niche overlap, Pianka's index (Pianka 1973) was used:

$O_{jk} = \Sigma (p_{ij} * p_{ik}) / [\sqrt{\Sigma p_{ij}^2 * \Sigma p_{ik}^2}]$ where O_{jk} is Pianka's measure for niche overlap between predator *j* and predator *k*, p_{ij} is the proportion of prey type *i* in relation to the total amount of prey ingested by predator *j*, p_{ik} is the proportion of prey type *i* in relation to the total amount of prey consumed by predator *k*, and m is the total number of prey types. The calculations were based on the relative biomass of the prey types.

The index ranges from 0, i.e. no overlap, to 1, i.e. complete overlap.

Dataset accuracy

The use of re-sampling techniques (e.g. bootstrapping) to produce confidence intervals around estimates of dietary composition (Reynolds & Aebischer 1991) are used to avoid misleading conclusions about elusive, difficult to observe and occurring in low population densities predator feeding habits (Davis et al 2012). For evaluating the accuracy in our conclusions, we generated the confidence intervals of each year as well as seasons by bootstrapping. We used a parametric bootstrap approach to calculate variances for the diet of each year, calculated 10,000 bootstrap estimates to obtain the standard error for the estimated diet components and examined the mean of the bootstrap distribution to assess bias in the estimates (Efron and Tibshirani 1993). Bootstrapping is a technique that has previously been useful in the analysis of predator diets (e.g. Karanth and Sunqvist 1995; Davis et al 2012).

Prey density, estimation of human harvesting and predation

In SCA, moose density was on average 1.26/ km^2 and roe deer density on average 0.57/ km^2 from pellet counts in 7 of the territories (Eriksen et al 2009; Sand et al 2012; Gervasi et al 2012). The average prey densities in the three Tuscan areas showed that roe deer had the highest density of 25.8 individuals/km^2, wild boar 7.41/ km^2, fallow deer 2.86/ km^2, red deer 1.91/ km^2, and mouflon 3.25/ km^2. Roe deer and wild boar were ubiquitous whether the other species occurred just in one or two study areas. Estimates were calculated by drive censuses and vantage point methods.

Statistical analysis

As wolves are highly mobile and move across territorial borders and long distances, scat samples were considered independent although some may have come from the same resident individual. When normally distributed, statistical significance was tested with independent samples *t* test, ANOVA and post-hoc Tukey HSD test. When data was not normally distributed, Mann Whitney and Kruskal Wallis tests were used. Data was analysed using IBM SPSS Statistics 21 and StatSoft Statistica 10, R for bootstrapping.

Results

In SCA, a total of 2159 scats were collected and analysed from 20 wolf territories (two of them on the Norwegian side), between 1997 and 2006. 803 were collected in summer and 1334 in winter. Of these, 90.5% contained wild ungulates, 4.6% small mammals, 1.1% rodents/insectivores, 0.7% birds, 0.5% domestic animals, 0.6% other prey and 2.5% vegetarian (berries and grass). In TUS, a total of 542 scats were collected and analysed 2005-2009 of which; 266 in Alpe di Catenaia, 156 in Val di Cecina (Berignone) and 120 in Orecchiella. Of these, 268 were collected during summer and 274 during winter. Scat content contained 89.8% wild ungulates, 0.7% small mammals, 0.7% rodents/insectivores, 3.2% domestic animals, 1% other preys and 5.5% vegetarian (fruit, berries and grass) (Table 1).

In both study areas, wolf diet composition is clearly dominated by wild ungulates. The remaining minor categories were, in the order, small mammals and vegetation in SCA and vegetation and domestic animals in TUS. TUS had highest scat collection activity with 0.6 scats collected per km^2 (542 scats from 896 km^2) and SCA 0.12 per km^2 (2159 scats from 17,370 km^2). From the bootstrapping resample, it is possible to notice that the Swedish dataset showed a continuous and stable image from 1997-2006 with negligible temporal, prey species-specific or food item variance. On the contrary, the Tuscan dataset 2005-2009 (excluding 2007) differed conspicuously, in variance. According to the three different equations (Tab. 2), the level of biomass differs most strongly with Floyds equation, which shows a higher intake per scat. In this study, where moose is the main prey in SCA and wild boar in TUS, it may be appropriate to compare all the three equations for a comprehensive view. In terms of biomass intake, SCA had the highest biomass found in wild ungulates 97.3% and minor parts from small mammals 2.46% and domestic animals 0.24%. TUS also had the highest level of biomass found in wild ungulates 94.76%,

followed by domestic animals 4.35% and small mammals 0.89%.

Using Manly's alpha preference index, wolves in SCA clearly showed positive preference of moose and negative preference of roe deer and wolves in TUS showed positive preference of wild boar and mouflon and negative preference of roe deer, red deer and fallow deer (Tab. 1). Both roe deer in SCA, and wild boar in TUS are heavily hunted by humans in relation to their densities. Furthermore, there is a lower proportion of human harvest of moose in SCA and roe deer in TUS in relation their densities. Remarkable is the high number of available roe deer in Alpe di Catenaia after human predation, but relatively small part of the wolf diet compared to wild boar.

Niche width and overlap

Levin's Food Niche Breath was broader in TUS (B = 4,0) than in SCA (B = 2,5) and consequently higher standardised in TUS (B_A = 0.23) than in SCA (B_A = 0.12). This results in a higher niche overlap in SCA (O_{jk} = 0.85) than in Italy (O_{jk} = 0.63) using Pianka's index.

Seasonal prey age class variation

Our data clearly shows wide variations in seasonal prey age class variation. As demonstrated in Table 1, moose and wild boar are the most selected prey species, followed by roe deer in both study areas. However, when comparing summer and winter seasons (Tab. 3), the second prey choice in summer is more dynamic, explicitly in SCA. Not only prey species choice changes between the seasons. SCA clearly shows in a two-tailed Mann-Whitney test, significant increase in selection of moose calves: U = 1,443.5, n = 216, 18, P =0.05. Second prey choice was undetermined cervids but since other species than moose and roe deer are not common in the wolf territories, many of these were most likely moose or roe deer. Other mammals were mainly consumed during summer as well as the small amount of domestic prey. During winter, roe deer fawn were never found. Similar pattern was also shown in Tuscany, where all cervid fawns increased in summer (U = 2.5, n = 7, 1, P <0.564), as did adult fallow deer and adult mouflon (U = 2.0, n = 3, 2, P =0.519). In SCA the main source of biomass consumed was by one third from moose during summer, and nearly exclusively during winter. The other prey species were fairly evenly distributed with domestic animals contributing with the second highest levels of biomass during summer and roe deer during winter. Also bootstrap simulations showed low variation in the two seasons of the Scandinavian data.

In TUS wild boar was the highest selected all year round, especially young 10-35 kg during winter. During summer there was no significant difference between young 10-35 kg and adults. Roe deer was the secondly selected prey species. Fallow deer, mouflon and red deer increased during summer, in relation to fawning season. Highest source of biomass in TUS came primarily from wild boar and secondly from roe deer all seasons, closely followed by fallow deer during the summer season. All other ungulate species as well as domestic species, had a fairly evenly distribution as biomass source during the winter season. Bootstrap simulations showed higher variation between the different prey species in TUS compared to south-central SCA with the highest variation within species in the summer seasons.

1. Wolf consumption in Sweden and Italy. Frequency of occurrence in scats (FO/S), frequency of occurrence of item (FO/I), *n* of scats and %. Whole Scat Equivalent (WSE) summarising the relative dry volume for a given food item within the scat sample. Average all seasons assumed prey weight, prey density/km², prey selection by Manley's preference index α, human hunting harvest/km² reported by the Swedish Hunters Association for Hunting and Wildlife Management 2005-2009 in the counties, and local hunting teams in Alpe di Catenaia (no hunting reports available from Orecchiella or Berignone). Availability/km² is prey density/km² after human predation available for wolf. * selective, ** negative selection, *** inadequate number of records reported

food item	FO/S						FO/I						weigh			density	human hunt	availability	selection	bootstrap 95% CI	
	summer n	*summer %*	*winter n*	*winter %*	*total n*	*all seasons %*	*summer n*	*summer %*	*winter n*	*winter %*	*total n*	*all seasons %*	*summer*	*winter*	*all seasons*	*ind/km2*	*/km2*	*/km2*	*Manly's α*	*lower*	*upper*
SOUTH-CENTRAL SCANDINAVIA																					
moose *Alces alces*	581	53,4	1031	67,3	1612	61,6	499,6	65,09	968,18	78,80	1468	73,5	116,7	192,0	160,6	1,26	0,36	0,9	0,79 *	90,87	91,60
undetermined cervid *Cervidae*	113	10,4	147	9,6	260	9,9	91	11,86	126,81	10,32	218	10,9					0,47	0,1	0,21**	83,76	84,18
roe deer *Capreolus capreolus*	67	6,2	127	8,3	194	7,4	54,5	7,10	119,2	9,70	174	8,7	17,1	20,0	18,8	0,57				89,45	89,77
beaver *Castor fiber*	41	3,8	27	1,8	68	2,6	31,1	4,05	0,2	0,02	31	1,6	18,0	18,0	18,0					75,72	75,74
hare *Lepus europaeus*	19	1,7	22	1,4	41	1,6	10,5	1,37	0,12	0,01	11	0,5	3,5	3,5	3,5					55,38	55,50
badger *Meles meles*	28	2,6	5	0,3	33	1,3	16,9	2,20	3,31	0,27	20	1,0	10,5	10,5	10,5					61,21	61,22
rodents *Rodentia, Insectivora*	37	3,4	36	2,4	73	2,8	13	1,69	0,11	0,01	13	0,7	0,0	0,0	0,025					32,31	32,32
birds *Aves*	38	3,5	46	3,0	84	3,2	6,3	0,82	9,25	0,75	16	0,8								18,46	18,52
insects	39	3,6	6	0,4	45	1,7		0,00	0,06	0,00	0	0,0									
undetermined carnivore *Carnivora*	6	0,6	9	0,6	15	0,6	4,9	0,64	0,04	0,00	5	0,2									
undetermined mammal *Mammalia*		0,0	2	0,1	2	0,1	0,5	0,07	0,01	0,00	1	0,0									
domestic animals	14	1,3	1	0,1	15	0,6	9,7	1,26	1	0,08	11	0,5	25,0	25,0	25,0					70,99	71,01
fruit/berries	31	2,8	17	1,1	48	1,8	4,4	0,57	0,02	0,00	4	0,2									
plant material	70	6,4	53	3,5	123	4,7	22,9	2,98	0,21	0,02	23	1,2									
wolf (grooming)	4	0,4	2	0,1	6	0,2	2,2	0,29	0,15	0,01	2	0,1									
non food items																					
TOTAL	1088		1531		2619		767,5		1228,67		1996										
TUSCANY																					
wild boar *Sus scrofa*	112	38,49	134	45,12	246	41,8	87,5	32,47	123,25	48,24	210,75	40,1	36,1	33,8	35,0	6,91	5,89	1,52	0,36 *	38,64	39,13
roe deer *Capreolus capreolus*	37	12,71	82	27,61	119	20,2	59,75	22,17	70,75	27,69	130,5	24,9	27,8	24,6	26,2	25,1	3,64	22,16	0,063**	23,88	24,28
red deer *Cervus elaphus*	20	6,87	7	2,36	27	4,6	18,5	6,86	7	2,74	25,5	4,9	39,1	102,5	70,8	1,91	***		0,169**	4,66	4,75
fallow deer *Dama dama*	40	13,75	18	6,06	58	9,9	37,75	14,01	14,75	5,77	52,5	10,0	23,9	55,4	39,7	2,86	***		0,074**	12,35	12,54
moufflon *Ovis orientalis*	27	9,28	15	5,05	42	7,1	24,5	9,09	14,25	5,58	38,75	7,4	22,9	23,8	23,4	4,88	***		0,33 *	7,08	7,22
hare *Lepus europaeus*	2	0,69	2	0,67	4	0,7	4	1,48	1,5	0,59	5,5	1,0	3,0	3,0	3					0,64	0,65
rodents *Rodentia, Insectivora*	4	1,37	1	0,34	5	0,9	6,5	2,41	0,25	0,10	6,75	1,3	0,0	0,0	0,03					0,64	0,65
domestic animal	10	3,44	8	2,69	18	3,1	9	3,34	7,5	2,94	16,5	3,1	55,8	55,8	55,8					3,01	3,08
fruit/berries	15	5,15	4	1,35	19	3,2	9	3,34	2,5	0,98	11,5	2,2								2,09	2,16
plant material	20	6,87	19	6,40	39	6,6	9	3,34	7,75	3,03	16,75	3,2								3,02	3,16
fox *Vulpes vulpes*	2	0,69	1	0,34	3	0,5	2	0,74	1	0,39	3	0,6									
mustelid *Mustelidae*	0	0,00	2	0,67	2	0,3	0	0,00	2	0,78	2	0,4									
non identified	2	0,69	1	0,34	3	0,5	2	0,74	1	0,39	3	0,6								0,55	0,56
other	0	0,00	3	1,01	3	0,5	0	0,00	2	0,78	2	0,4								0,36	0,37
TOTAL	291		297		588		269,5		255,5		525										

Table 2. Whole Scat Equivalents and Average Volume summarizing the relative dry volume for a given food item within the scat sample. Biomass consumed per scat, in kg and per cent all seasons using three equations by Floyd et al 1978, Weaver 1993 and Rüehe et al 2003. Calculations are presented with the Floyd equation: y = 0,383 + 0,02x, Weaver equation: y = 0,439 + 0,008x and Rüehe equation y = 0,731 + 0,00406x when x is the assumed average weight

		Floyd			**Weaver**			**Rüehe**		
SCANDINAVIA	%WSE	*kg/scat*	*kg*	*%*	*kg/scat*	*kg*	*%*	*kg/scat*	*kg*	*%*
moose	0,796	3,60	6117,6	95,57	1,72	2933,3	92,50	1,38	2353,3	87,31
roe deer	0,094	0,76	153,2	2,39	0,59	118,9	3,75	0,81	162,9	6,04
small mammals	0,013	0,38	10,4	0,16	0,44	11,9	0,38	0,73	19,8	0,74
beaver	0,029	0,74	45,3	0,71	0,58	35,5	1,12	0,80	49,0	1,82
hare	0,052	0,45	49,9	0,78	0,47	51,5	1,62	0,75	82,2	3,05
badger	0,011	0,59	13,8	0,22	0,52	12,1	0,38	0,77	18,0	0,67
domestic animals	0,006	0,88	10,8	0,17	0,64	7,8	0,25	0,83	10,2	0,38
			6400,9			3171,1			2695,4	
ITALY	%AV									
wild boar	0,438	1,08	256,7	44,31	0,72	170,5	44,10	0,87	207,1	43,91
roe deer	0,271	0,91	133,2	23,00	0,65	95,3	24,65	0,84	123,0	26,08
red deer	0,053	1,80	51,6	8,92	1,01	28,9	7,46	1,02	29,2	6,20
fallow deer	0,109	1,18	69,5	12,00	0,76	44,7	11,56	0,89	52,7	11,18
mouflon	0,080	0,85	37,1	6,40	0,63	27,3	7,06	0,83	36,0	7,64
hare	0,007	0,44	1,7	0,30	0,46	1,8	0,47	0,74	2,9	0,62
small mammals	0,007	0,38	1,5	0,26	0,44	1,7	0,45	0,73	2,9	0,61
domestic animal	0,034	1,50	27,8	4,81	0,89	16,4	4,25	0,96	17,8	3,77
			579,2			386,6			471,7	

Tab. 3. Assumed prey weight, Whole Scat Equivalence/average volume and estimation of consumed biomass in kg and per cent in south-central Sweden and Tuscany calculated using the Weaver equation (Weaver 1993) during summer May-September in Sweden and winter October-April in Italy.

	Summer					Winter				
SWEDEN	assumed weight (kg)	WSE / AV%	biomass consumed/scat (kg)	biomass consumed (kg)	biomass consumed (%)	assumed weight (kg)	WSE / AV%	biomass consumed/scat (kg)	biomass consumed (kg)	biomass consumed (%)
moose	116,7	78,7	1,37	1102,2	29,8	192	85,3	1,98	2248,4	95,2
roe deer	17,1	8,6	0,58	462,4	12,5	20	10,5	0,60	83,9	3,6
beaver	18	1,6	0,58	468,1	12,7	18	1,1	0,58	8,4	0,4
hare	3,5	2,7	0,47	375,0	10,2	3,5	0,3	0,47	1,8	0,1
badger	10,5	1,5	0,52	420,0	11,4	10,5	0,1	0,52	0,6	0,0
domestic	25	2,0	0,64	513,1	13,9	25	1,0	0,64	8,0	0,3
rodents	0,025	4,9	0,44	352,7	9,5	0,025	1,8		10,3	0,4
				3693,5					2361,5	
TUSCANY										
wild boar	36,1	36,1	0,73	70,5	38,3	33,8	51,52	0,70	100,1	53,2
roe deer	27,8	24,7	0,66	43,7	23,7	24,6	29,57	0,60	51,5	27,4
red deer	39,1	7,6	0,75	15,4	8,4	102,5	2,93	1,30	10,1	5,4
fallow deer	23,9	15,6	0,63	26,3	14,3	55,4	6,17	0,50	7,7	4,1
mouflon	22,9	10,1	0,62	16,9	9,2	23,8	5,96	0,60	10,3	5,5
hare	3,0	0,8	0,46	1,0	0,6	3	0,63	0,50	0,8	0,4
rodents	0,0	1,3	0,44	1,6	0,9	0,03	0,1	0,40	0,1	0,1
domestic	55,8	3,7	0,89	8,8	4,8	55,8	3,13	0,90	7,6	4
				184,2					188,3	

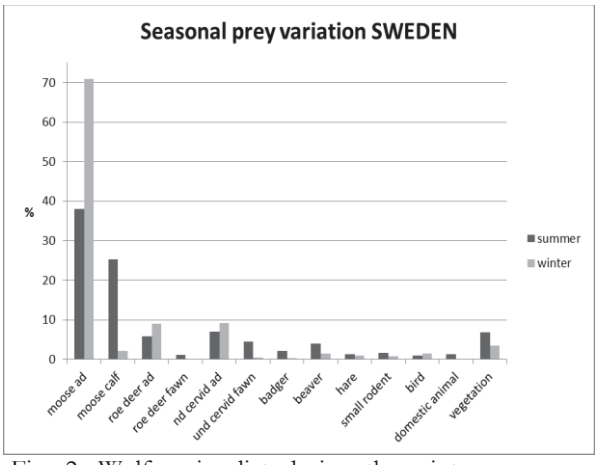

Fig. 2. Wolf main diet during the winter season consists of adult moose and moose calf during the summer. Other species than cervids also increase during the summer season.

Territorial variances

Calculating each territory separately, Table 4 shows the variance within SCA and TUS. In SCA, moose is the strongest selected prey species all seasons except for in two territories where roe deer is the strongest selected prey species during winter. TUS had higher variation showing strong selection of wild boar all seasons and also red deer during summer in Alpe di Catenaia, mouflon all seasons and also red deer during summer in Orecchiella and both fallow deer and mouflon all seasons in Berignone. On average, the SCA territories showed higher niche width in the winter season while similar niche width all seasons in TUS. However, the variance was higher during summer in TUS. Niche overlap had higher variance in SCA during summer and lower in TUS.

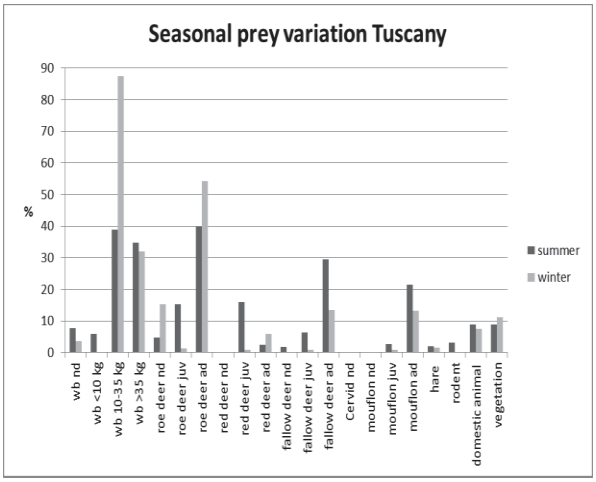

Fig. 3. Wild boar 10-35 kg is the main prey type during winter, followed by adult roe deer. During summer, juvenile and adult wild boar and adult roe deer are chosen equally as well as an increase in other ungulates. Significant increase in roe and red deer fawn during summer (paired sample *t* test: $t_{270} = 3.68$, $P = 0.00014$ and $t_{270} = 3.80$, $P < 0.0001$).

Tab. 4. Seasonal numbers of scat samples containing prey species with known density in each territory in SCA and TUS. Territories with none or very few samples collected in either summer or winter were excluded. Pianka's index shows niche overlap, Levins Food Niche Breadth, FNB, shows possible food resources and Manly's Alpha shows selectivity. The equations are all expressed in a scale from 0 - 1, 0 beeing none to 1 being complete.

			Manly's α	**Levins FNB**	**Pianka's index**
SCANDINAVIA		*n*	preference	niche width	niche overlap
Bograngen	summer	36	moose 0.87	0.3991	0.727
	winter	24	no roe deer	0.4347	0.7731
	all seasons		*moose 0.91*		
Dals-Ed	summer	73	moose 0.68	0.3341	0.8331
	winter	34	roe deer 0.72	0.381	0.7612
	all seasons		*roe deer 0.51*		
Filipstad	summer	21	moose 0.78	0.3197	0.7378
	winter	50	moose 0.8	0.1709	0.8607
	all seasons		*moose 0.8*		
Grangärde/Gravendal/ Glaskogen	summer	76	moose 0.74	-0.071	0.4118
	winter	217	moose 0.81	0.1824	0.8401
	all seasons		*moose 0.79*		
Hagfors	summer	100	moose 0.8	0.2604	0.7527
	winter	81	moose 0.82	0.154	0.8576
	all seasons		*moose 0.81*		
Hasselfors	summer	72	moose 0.69	0.2347	0.7665
	winter	205	moose 0.65	0.256	0.8519
	all seasons		*moose 0.66*		
Leksand	summer	111	moose 0.87	0.1617	0.4859
	winter	280	moose 0.89	0.0987	0.8484
	all seasons		*moose 0.89*		
Nyskoga	summer	93	moose 0.94	0.102	0.7348
	winter	123	moose 0.96	0.0835	0.8521
	all seasons		*moose 0.95*		
Tisjön	summer	84	moose 0.96	0.2208	0.7723
	winter	48	moose 0.75	0.3957	0.8229
	all seasons		*moose 0.87*		
Tyngsjö	summer	15	no roe deer	-0.098	0.4552
	winter	110	moose 0.92	0.1601	0.8443
	all seasons		*moose 0.93*		
Årjäng	summer	48	moose 0.77	0.2789	0.7826
	winter	6	no roe deer	0.8	0.7404
	all seasons		*moose 0.79*		
Våler, Norway	summer	73	moose 0.65	0.3228	0.8381
	winter	9	roe deer 0.77	0.8406	0.6802
	all seasons		*moose 0.6*		
TUSCANY					
Alpe di Catenaia	summer	129	wild boar 0.69, red deer 0.38	-0.13	0.6149
	winter	152	wild boar 0.75	0.1362	0.6009
	all seasons		*wild boar 0.69*		
Orecchiella	summer	55	red deer 0.46, mouflon 0.8	1.109	0.8121
	winter	66	mouflon 0.41	0.5613	0.7222
	all seasons		*mouflon 0.57*		
Val di Cecina (Berignone)	summer	98	fallow deer 0.47, mouflon 0.44	0.379	0.7013
	winter	47	fallow deer 0.3, mouflon 0.28	0.6419	0.8646
	all seasons		*fallow deer 0.41, mouflon 0.39*		

Discussion

Density angd age class dependent prey selection

The results in this study confirmed that the major component of wolf diet comes from wild ungulates followed by a minor part of small mammals and domestic animals (Mattioli et al 1995; Okarma 1995; Jedrzejewski et al 2000; Sand et al 2005; Stahler et al 2006). As we expected, moose was the main prey in Swedish wolf diet, having the highest density values. The proportion of moose calf increased from 3% during winter to 40% during summer, even though the largest part of the scat content consisted of adult moose. Caution should be taken however to the period after the first moulting to the time the calf becomes a yearling as it is difficult to classify exact age during their first winter. Some scats classified as adults during winter may have been calves after the first moult. Calves offer a relatively small amount of biomass per kill which results in a higher kill rate per time unit during the vegetative growth period. However, body size increases rapidly resulting in higher biomass intake per kill for predators. The most abundant prey species was however not selected in Italy where the most common prey species, wild boar, had only one third of the density compared to the second selected prey species, roe deer. In Alpe di Catenaia, wild boar was also heavily hunted by humans, resulting in fewer individuals available for wolves. Nonetheless, wild boar was the most selected prey species there but not in the two other Tuscan areas as demonstrated with Manly's Alpha preference index. Seasonal variation in different age classes (Fig. 2) showed that young wild boar and adult roe deer are clearly selected during winter, whereas there is a more varied distribution of prey selection during summer, covering several species. This generated changes in prey composition and density of the sample through the years. Moreover, this is obviously related to the strongly different ungulate communities of the three areas taken into account and to the different time spans covered by the collection in the three areas. Thus, for the Tuscan areas, our first prediction was not supported by the data analysis as roe deer had the highest density of all prey species, yet wild boar, mouflon and fallow deer were the most selected. Predator-prey ratio and predation rate contributes to the demographic impact of predation. Selection of prey age classes, and seasonal variation in predation pressure acts differently on prey species why simply numerical relations between predator and prey are an insufficient measurement of predation level (Gervasi et al 2012). Age classes in different seasons in this study are presented (Fig. 2 and 3) for a clarified overview of the increased selection of cervid fawns during summer.

Determination of landscape changes

In SCA, forest land is the most commonly occurring category of land type, accounting for 53 %, which has not changed significantly since 2000. The trend over a ten-year period, 1995-2005, has been towards a gradual reduction in the acreage of arable land (Swedish Environmental Protection Agency). Karlsson et al (2007) analysed wolf habitat variables and determined that there was a significant decline in the proportion of built-up areas within the wolf territories, but no significant change for open land or local road density. The Apennine ecosystem is changing in recent decades due to abandonment of traditional farming and forest activities and the increase in forest coverage. This process has been accelerated by the European Union regarding nature conservation and rural development (Agnoletti 2007; Pelorosso et al 2009, Geri et al 2010), which benefits ungulates as well as wolves who prefers areas with high forest cover, few roads and low human density (Mech et al 1988). Minor changes has been taking place in SCA but compared to TUS and especially the Tuscan Apennines, the wolf habitat is more dynamic in the sense of landscape changes and increase of prey abundance. These are positive changes for the wolf population and the co-existence with the dense human density is somewhat eased in the Tuscan Apennines. Different latitudes may reflect on habitat heterogeneity, however, the level of human utilisation of the landscape determines wolf diet diversification too. The intensively exploited forest industry in SCA prevents rich species diversity, opposing to the abandoned former agricultural areas in the Apennines, allowing re-forestation and species diversification. The outcome may lead to increased variation in predator-prey relationships

due to a more extensive heterogeneity in TUS compared to south-central SCA.

Influence of size on selection

The body size difference in Swedish and Italian wolves was not the only reason for Italian wolves predating on smaller ungulate species. Wild boar in TUS are relatively small compared to northern European, adults weighing 66.5 ± 0.48 kg (based on mass data for 1286 wild boar carcasses collected by the Province of Arezzo). Our second prediction that Italian wolves choose smaller prey species is supported by this study. However, no larger ungulates than red deer are present in TUS and choosing young wild boar during winter may suggest that they are not only preferred due to lack of experience and anti-predator behaviour. Optimal foraging strategy, described by Stephen and Krebs (1986), highlights the importance of predators' selection of the most profitable prey, profitability being the ratio between energy gain and handling time. Depending on the prey species density, encounters may occur frequently or rarely and the time and risk when killing varies with prey size and behaviour. Moreover, within a prey species, there are differences in sex-, age- and size groups which affects kill rate and risk of injury. Adult wild boar can cause serious injury or death to predators, and albeit the Apennine wild boar is somewhat smaller than in other parts of Europe, it can be energy beneficial targeting younger individuals. There was no significant seasonal difference (independent samples *t* test) in adult wild boar predation and Tuscan wolves switch seasonally to mainly other ungulates than wild boar during the summer season. Moose can also cause injury to predators but as the Scandinavian moose are naïve due to a long period of wolf absence, their anti-predator behaviour has not yet had enough time to adjust to the re-colonising wolves (Sand et al 2006a). In spite of negative preference using Manly's Alpha preference index, roe deer is the second prey selection as well as the second largest source of biomass in both south-central SCA and TUS with the exception of summer in SCA. When present at high density, roe deer can be a profitable prey for wolves because of the high encounter rate and low handling time (Huggard 1993; Mattioli et al 2004; Sand et al 2005), nevertheless, roe deer selection was low in TUS in relation to their density. As shown in the Serengeti ecosystem, predation pressure is higher on small herbivore ungulates, less than 150 kg, and they also suffer predation from more predators than large ungulates (Sinclair et al 2003). Besides predation risk from wolf, brown bear and red fox, vigilance may be higher in Swedish roe deer as another predator, Eurasian lynx, is a stalking predator forcing higher anti-predator behaviour investment. In TUS however, roe deer has only two predators, wolf and red fox (Bassi et al 2012), the latter predating solely on fawns during the first weeks post-birth (Jarnemo & Liberg 2005). It has been shown that wolves hunting success is lower due to longer chase distance, fewer encounters and less predator-naïve behaviour in roe deer than in moose in SCA (Wikenros et al 2009), but no similar studies published from Italy. Conclusively, moose is a larger prey species in relation to the SCAn wolves, nearly four times, compared to wild boar in relation to the Italian wolves which are virtually equal in weight, calculated all seasons. We argue that the increase of moose calf in wolf diet in SCA during summer, and the increase of young wild boar in TUS during winter, associates with the size difference relation between predator and prey. When winter comes, moose calves are larger in proportion to Scandinavian wolves, than young wild boar in relation to Tuscan wolves. The risk of injury from young wild boar 10-35 kg is not as high as the risk of injury from a young moose 120-162 kg. However, wild boar in TUS has no fixed reproduction season, even if many

parturitions takes place in spring. During summer in SCA, moose calves are easy to catch with less risk of injury than adults. With the risk of injury from wild boar in TUS, wolf selection of young and adult cervids during summer may be explained by ungulate females rearing young, adapting a hider strategy, are less mobile, thus easier to encounter and without risk of injury.

Human density affect

The human factor affecting predators were clearly shown as TUS has higher human density and higher road density compared to south-central SCA. The proportion of domestic animals in wolf diet was 3.2% in TUS and 0.5% in SCA, which showed higher depredation in TUS. In Italy, due to the common practice of free-ranging domestic animals during the summer season in the mountain pastures, it may be an easy food source if not guarded by shepherds, guard dogs or fence. Wolves seem to selected especially sheep rather than kill livestock randomly, since they are easy to kill (Gula 2008). In Sweden, there are almost no free-ranging domestic animals. Our prediction that higher human density would result in higher depredation appears to be the case but the reason for this may well be the different approaches of animal husbandry, not prey abundance and density.

Acknowledgements

We thank all people who through the years helped collecting wolf scats in field and laboratory analysis. We also thank Sabrina Müller, Stefania Boschettos and Dr Cecilia Ambrogi who shared some of the data from their master thesis, scat collection and data analysis. Thanks to Dr Håkan Sand who provided very valuable comments on an earlier version of the manuscript. The study was funded practical and financial by Arezzo Province, Axel and Margaret Ax:on Johnsons Foundation and Helge Ax:on Johnsons Foundation.

References

Agnoletti, M. 2007. The degradation of traditional landscape in a mountain area of Tuscany during the 19th and 20th centuries: Implications for biodiversity and sustainable management. Forest Ecology And Management. 249:1-2, 5-17.

Angerbjörn, A., Tannerfeldt, M., Erlinge, S. 1999. Predator-prey relationships: Arctic foxes and lemmings. Journal of Animal Ecology 68:34-49.

Bassi, E., Donaggio, E., Marcon, A., Scandura, M., Apollonio, M. 2012. Trophic niche overlap and wild ungulate consumption by red fox in a mountain area in Italy. Mammalian Biology, 77:369-376.

Capitani, C., Bertelli, P., Varuzza, M., Scandura, M., Apollonio, M. 2004. A comparative analysis of wolf diet in three different Italian ecosystems. Mammalian Biology, 69:1-10.

Chesson, J. 1978. Measuring preference in selective predation. Ecology 59:211-215.

Ciucci, P., Boitani, L., Pelliccioni, E.R., Rocco, M., Guy, I. 1996. A comparison of scat analysis methods to access the diet of the wolf *Canis lupus*. Wildlife Biology, 2:37-48.

Darimont, C.T., Reimchen, T.E., Paquet, P.C. 2003. Foraging behviour by grey wolves on salmon streams in coastal British Columbia. Can. J. Zool. 81:349-353.

Davis, M.L., Stephens, P.A., Willis, S.G., Bassi, E., Marcon, A., Donaggio, E., Apollonio, M. 2012. Prey Selection by an Apex Predator: The Importance of Sampling Uncertainty. PLoS ONE 7:e478

Debrot S. 1982. Atlas des poils de Mammifieres d'Europe. Peseux, Suisse. 208 pp.

Efron & Tibshirani 1993. An Introduction to the Bootstrap. Chapman and Hall, New York.

Eriksen, A. Wabakken, P., Zimmermann, B., Andreassen, H.P., Arnemo, J.M., Gundersen, H., Milner, J.M., Liberg, O., Linnell, J., Pedersen, H.C., Sand, H., Solberg, E.J., Storaas, T. 2009. Encounter frequencies between GPS-collared wolves *(Canis lupus)* and moose *(Alces alces)* in a Scandinavian wolf territory. Ecological Research, 24: 547–557.

Fabbri, E., Miquel, C., Lucchini, V., et al. 2007. From the Apennines to the Alps: colonization genetics of the naturally expanding Italian wolf (Canis lupus) population. Molecular Ecology, 16:1661-1671.

Feldhamer, G.A., Farris-Renner, K.C., Barker, C.M. 1988. Mammalian Species, 317:1-8.

Gazzola, A., Avanzinelli, E., Bertelli, I., Tolosano, A., Bertotto, P., Musso, R., Apollonio, M. 2007. The role of the wolf in shaping a multi-species ungulate community in the Italian western Alps. Italian Journal of Zoology 74:297-307.

Geri, F., Amici, V., Rocchini, D. 2010. Human activity impact on the heterogeneity of a Mediterranean landscape. Applied Geography, 30:370-379.

Gervasi, V., Nilsen, E.B, Sand, H., Panzacchi, M., Rauset, G.R., Pedersen, H.C., Kindberg, J., Wabakken, P., Zimmermann, B., Odden, J. Liberg, O., Swenson, J.E. and Linnell, J.D.C. 2012. Predicting the potential demographic impact of predators on their prey: a comparative analysis of two carnivore–ungulate systems in SCA. Journal of Animal Ecology 2012, 81, 443–454.

Gula, R. 2008. Wolf depredation on domestic animals in the Polish Carpathian Mountains. Journal of Wildlife Management, 72:283-289.

Haglund, B. 1968. Winter habits of large carnivores. Viltrevy, 5: 213–361. [In Swedish with English summary]

Holling, C.S. 1959*a*. The components of predation as revealed by a study of small-mammal predation of the European pine sawfly. Canadian Entomologist, 91:293-320.

Holling, C.S. 1959*b*. Some characteristics of simple types of predation and parasitism. Canadian Entomologist, 91:385-398.

Huggard, D.J. 1993. Prey selectivity of wolves in Banff National Park. I. Prey species. Canadian Journal of Zoology, 71:130–139.

Jarnemo, A. and Liberg, O. 2005. Red Fox Removal and Roe Deer Fawn Survival: A 14-Year Study. The Journal of Wildlife Management, 69:1090-1098.

Jedrzejewski, W., Jedrzejewska, B., Okarma, H., Schimdt, K., Zub, K., Musiani, M. 2000. Prey selection and predation by wolves in Bialowieza Primeval Forest, Poland. Journal of Mammalogy: 81:197-212.

Karanth, K.U. and Sunquist, M.E. 1995. Prey Selection by Tiger, Leopard and Dhole in Tropical Forests. Journal of Animal Ecology, 64:4: 439-450.

Karlsson, J., Brøseth, H., Sand, H. and Andrén, H. 2007. Predicting occurrence of wolf territories in Scandinavia. Journal of Zoology, 727: 276-283.

Levins R. 1968. Evolution in changing environments. Princeton University Press, Princeton.

MacArthur R.H. and Pianka, E.R. 1966. On optimal use of a patchy environment. American Naturalist, 100:603-609 .

Mattioli, L., Apollonio, M., Mazzarone, V., Centofanti, E. 1995. Wolf food habits and wild ungulate availability in the Foreste Casentinesi National Park, Italy. Acta Theriologica, 40: 387-402.

Mattioli, L., Capitani, C., Gazzola, A., 2011. Prey selection and dietary response by wolves in a high-density multi-species ungulate community. European Journal of Wildlife Research,57:909-922.

McElligott, A.G., Gammell, M.P., Harty, H.C., Paini, D.R., Murphy, D.T., Walsh, J.T., Hayden, T.J. 2001. Sexual Size Dimorphism in Fallow Deer *(Dama dama):* Do Larger, Heavier Males Gain Greater Mating Success? Behavioral Ecology and Sociobiology, 49:266-272.

Mech, L.D., Fritts, S.H., Radde G.L. and Paul, W.J. 1988. Wolf distribution and road density in Minnesota. Wildlife Society Bulletin, 16:85-87.

Meriggi, A., Brangi, A., Schenone, L., Signorelli, D. & Milanesi, P. 2011. Changes of wolf (*Canis lupus*) diet in Italy in relation to the increase of wild ungulate abundance, Ethology Ecology & Evolution, 23:3, 195-210.

Milanesi, P., Meriggi, A. & Merli, E. 2012. Selection of wild ungulates by wolves Canis lupus (L. 1758) in an area of the Northern Apennines (North Italy), Ethology Ecology & Evolution, 24:1, 81-96.

Mitchell, B., Mccowan, D. and Nicholson, I.A. 1976. Annual cycles of body-weight and condition in Scottish-red deer *Cervus elaphus*.

Journal of Zoology, 180:107-127.

Moore, T.D, Spencer, L.E., Dugnolle, C.E., Hepworth, W.G. 1974. Identification of dorsal guard hairs of some mammals in Wyoming. Wyoming Game and Fish Department, Cheyenne, 14:177.

Okarma, H. 1995. The trophic ecology of wolves and their predatory role in ungulate communities of forest ecosystems in Europe. Acta Theriologica, 40:335-386.

Olsson, O., Wirtberg, J., Andsson, M., Wirtberg, I. 1997. Wolf *Canis lupus* predation on moose *Alces alces* and roe deer *Capreolus capreolus* in south-central Scandinavia. Wildlife Biology 3: 13-25.

Pedersen, H.C., Wabakken, P., Arnemo, J.M., Brainerd, S.M., Brøseth, H., Gundersen, H.; Hjeljord, O., Libertg, O., Sand, H., Solberg, E.J., Storaas, T., Strømseth, T.H.; Wam H.; Zimmermann, B. 2005: Rovvilt og Samfunn (RoSa). Det skandinaviske ulveprosjektet – SKANDULV. Oversikt over glennomførte aktiviteter i 2000-2004. NINA Rapport 117. 78pp.

Pelorosso, R., Boccia, L., Amici, A. 2008. Simulating Brown hare (Lepus europaeus Pallas) dispersion: a tool for wildlife management of wide areas. Italian Journal Of Animal Science, 7:3, 335-350.

Peterson RO, Ciucci P. 2003. The wolf as a carnivore. In: Mech LD, Boitani L, editors. Wolves: behavior, ecology, and conservation. Chicago: University of Chicago Press; 2003.

Peterson, R.O., Woolington, J.D., Bailey, T.N. 1984. Wolves of the Kenai Peninsula, Alaska. Wildlife Monographs, 88: 52

Pianka, E.R. 1973. The structure of lizard communities. Annual Review of Ecology and Systematics, 4:53-74.

Reynolds, J.C. and Aebischer, N.J. 1991. Comparison and quantification of carnivore diet by fecal analysis - A critique, with recommendations, based on a study of the fox *Vulpes vulpes*. Mammal Review, 21: 97-122.

Russell, A.J.M and Storch, I. 2004. Summer food of sympatric red fox and pine marten in the German Alps. European Journal of Wildlife Research, 50:53-58.

Salvador, A. and Abad, P.L. 1987. Food habits of a wolf population *(Canis lupus)* in Leon Province, Spain. Mammalia Volume: 51 Issue: 1 Pages: 45-52.

Sand, H., Wabakken, P., Zimmermann, B., Johansson, Ö., Pedersen, H C., Liberg, O. 2008. Summer kill rates and predation pattern in a wolf-moose system: can we rely on winter estimates? Oecologia 156: 53–64.

Sand, H., Wikenros, C., Wabakken, P., Liberg, O. 2006*a*. Cross-continental differences in patterns of predation: will naive moose in Scandinavia ever learn? Proceedings of the Royal Society B 273: 1421–1427.

Sand, H., Vucetich, J.A., Zimmermann, B., Wabakken, P., Wikenros, C., Pedersen, H.C., Peterson, R.O., Liberg, O. 2012. Assessing the influence of prey–predator ratio, prey age structure and packs size on wolf kill rates. Oikos 121:1454–1463.

Sand, H., Zimmermann, B., Wabakken, P., Andrèn, H. and Pedersen, H.C. 2005. Using GPS technology and GIS cluster analyses to estimate kill rates in wolf–ungulate ecosystems. Wildlife Society Bulletin, 33:914–925.

Santiago-Moreno, J., González-Bulnes, A.,

Gómez-Brunet, A., Toledano-Díaz, A., López-Sebastián, A. 2005. Prediction of gestational age by transrectal ultrasonographic measurements in the mouflon *(Ovis gmelini musimon)*. Journal of Zoo and Wildlife Medicine, 36: 457-462.

Scandura, M., Apollonio, M. Mattioli, L. 2001. Recent recovery of the Italian wolf population: a genitic investigation using microsatellites. Mammalian Biology, 66:321-331.

Spaulding, R.L.; Krausman, P.R.; Ballard, W.B. 1997: Calculation of prey biomass consumed by wolves in northwest Alaska. Journal of Wildlife Research 2:128-132.

Stahler, D.R., Smith, D.W., Guernsey, D.S. 2006. Foraging and feeding ecology of the gray wolf *(Canis lupus):* Lessons from Yellowstone National Park, Wyoming, USA. Journal of Nutrition, 136:1923S-1926S.

Stephens, D.W and Krebs, J.R. 1986. Foraging theory. Princeton University Press, Chichester, West Sussex.

Teerink, B.J. 1991. Hair of west European mammals. Cambridge University Press, Cambridge. 224.

Wabakken, P., Aronson, Å., Strømseth, T.H., Sand, H., Maartmann, E., Svensson, L., Flagstad, O., Hedmark, E., Liberg, O., Kojola, I. 2009. The wolf in Scandinavia: status report of the 2009–2010 winter. Oppdragsrapport no. 4-–2010. Høgskolen i Hedmark, Elverum, Norway. (In Norwegian with English summary, figures and tables)

Wabakken, P., Sand, H., Liberg, O., Bjärvall, A. 2001. The recovery, distribution, and population dynamics of wolves on the Scandinavian peninsula, 1978-1998. Canadian Journal of Zoology 79: 710–725.

Watts, D.E., Butler, L.G., Dale, B.W. and Cox, R.D. 2010. The Ilnik wolf *Canis lupus* pack: use of marine mammals and offshore sea ice. Wildlife Biology 16:144-149.

Wikenros, C., Sand, H., Wabakken, P., Liberg, O., Pedersen, H.C. 2013. Wolf predation on moose and roe deer: chase distances and outcome of encounters. Acta Theriologica, 54:207-218.

PAPER III

Scavenger temporal and spatial selection of visits at feeding sites in north and south European wolf territories

SOPHIE STÅHLBERG AND MARCO APOLLONIO

Department of Natural and Environmental Science, University of Sassari, Via Muroni 25, Sassari 07100, Sassari, Italy.

Abstract

Temporal and spatial partitioning of feeding sites by members of scavenger guilds is required for avoiding predation and competition. Northern and southern European wolf habitats differ in species diversity and abundance, landscape type, climate and human impact. Camera traps were set inside wolf territories in south-central Sweden and in the Tuscan Apennines, Italy, for four years to observe scavengers tempo-spatial partitioning. Avian scavengers dominated the usage of carcasses followed by red fox in south-central Sweden while wild boar was the most visiting species followed by red fox in the Tuscan Apennines. However, wild boar did not scavenge on the carcass itself, but primarily on insects and arthropods around the carcass. We compared the most common visiting species and found a significant relationship in the 24 h activity pattern in red fox, badger and marten, but not in wolf or wild boar. In the seasonal activity pattern, only wolf was significantly correlated between the two areas. Feeding site characteristics such as visibility, snow coverage or vegetation coverage did not show any strong impact on site selection. 20.9% of the camera sites were located close to human disturbance in south-central Sweden and in 15.4% in the Tuscan Apennines. Red fox visited these in 39.2% of their visits while in Sweden 7.4% which may reflect on the higher human density in Italy. The typical scavenger pattern of utilising carrion as in alternative food resource in late winter was seen in more species in south-central Sweden than in the Tuscan Apennines which may indicate climate being an important factor in the feeding ecology of many scavenging species.

Key words: scavenger, intra-guild predation, temporal and spatial partitioning, movement triggered camera system

Introduction

Scavengers play an essential role in terrestrial ecosystems by accelerating the return of nutrients to trophic webs, distributing such nutrients over a wide area, and reducing potentially infective foci (DeVault et al 2003). In many ecosystems, it is likely that more energy is transferred through scavenging of carrion than through predation of live animals (Wilson and Wolkovich 2011), reflecting a major underestimation of the importance of carrion as a resource to vertebrate communities. The mortality factor of animal carcasses vary widely depending on different ecosystems abiotic factors; climate, soil, nutrient cycling, regeneration, forest fires and landslides, as well as biotic factors; herbivory, presence or absence of effective predators, human activity, disease and insect outbreaks (Houston 1979; Bergerud 1980; Frelich 2002; DeVault et al 2003). Scavengers, microbes, fungi and arthropods compete for cadaveric resources and the time of detection of the carcass is crucial. In cold climate regions or seasons when microbes, fungi and arthropods are less active, vertebrate scavengers monopolise the nutritional food source of carcasses (Putman 1983). Common vertebrate scavengers are birds, vultures being the only obligate scavenger, with excellent visual capability and availability of scanning large areas but mammals such as bears *(Ursus spp.)* and grey wolf *(Canis lupus)* may also gain advantage in arctic environments (Magoun 1976) where the lack of thermal uplifts reduces a bird's ability to soar efficiently or forested areas with limited visibility. Furthermore, large vertebrate

scavengers, which are frequently also facultative scavengers, have the ability to monopolise carrion when it is found (Green et al 1997) and exerts nocturnal activity when birds are inactive. Scavenging species may choose several food recourses with temporal-, spatial- and cost dependant variances, carrion being most available in late winter when many herbivore species suffer from food shortage, weakness and starvation. The use of carrion as a supplemental food resource during prey shortages may have substantial impacts on the population dynamics of predators and their prey (DeVault et al 2003). Carrion consumption may expose potential scavengers to risks such as disease (Jenelle et al 2009), conflicts with other scavengers (May et al 2008) and exposure to predation (Merkle et al 2009), yet the benefits of scavenging over predation may offset these risks. Large and medium sized scavenging species may be outcompeted by smaller sized though numerical superiority or aggregations, nonetheless, increments in carrion availability may allow scavenging species to reach higher densities by compressing home range sizes (Blàzquez et al 2009). Larger predators do kill intermediate predators when interfering at carcass sites (Lindström et al 1995; Berger & Gese 2007), however, smaller species may take advantage of larger predators by following or adjusting their behaviour temporarily or spatially (Macdonald et al 2004; Atwood & Gese 2010; Mattisson et al 2011). Small carcasses are usually consumed rapidly by scavengers (Travaini et al 1998; DeVault et al 2004), while in the temperate regions of the northern hemisphere, large carcasses may last several months (Green et al 1997).

Whereas carcasses produced from natural mortality is seasonally pulsed, wolf-killed prey species provide a more constant and predictable food resource for scavengers over the year (Wilmers et al. 2003; Selva & Fortuna 2007). In Yellowstone, wolf restoration has resulted in important changes on the ecosystem by altering the quantity and timing of carrion available to scavengers (Wilmers et al. 2003). Contrary to live prey, carcasses represent a food resource that may trigger inter- and intraspecific conflicts during feeding bouts at feeding sites. Thus, temporal and spatial segregation among species and individuals are necessary to avoid intraguild predation and conflict. As seen in previous studies (Wikenros et al 2013), temporal partitioning of the usage of food resources can be in a fine scale with only a few hours or minutes of differentiation.

This study includes data from north and south European wolf territories for a comparison of different climate regions and we describe the scavenging guild structure and the tempo-spatial partitioning of activity at feeding sites. The objective of this study was to find similarities and dissimilarities in scavenging species utilising feeding sites in wolf territories and in daily and seasonal activity patterns.

Material and methods

Ethics statement

The Swedish Animal Welfare Agency approved camera monitoring of scavenging species (Permit Number: C 51/9). Permission for camera monitoring of moose carcasses on both state-owned and privately owned land was obtained from the County Administrative Boards in Sweden (Dalarna (Permit Number: 211-14304-2006), Gävleborg (Permit Number: 211-1371-09), Värmland (Permit Number: 211-15846-06), Västmanland (Permit Number: 211-11827-06), and Örebro (Permit Number: 211-03990-2006)). All procedures including capture, handling and collaring of wolves (described in detail in Sand et al 2006), as well as camera monitoring of scavenging species, fulfilled the ethical requirements of the Swedish Animal Welfare Agency. Camera monitoring of scavenging species was approved by Arezzo Provincial Government.

Study areas

The two study areas were in south-central Sweden and in Alpe di Catenaia in the Tuscan Apennines, Italy (henceforth abbreviated SWE and IT).

SWE: wolf territories in the counties Värmland, Dalarna, Örebro, Västmanland and Gävleborg. (59-61°N, 12-17°E). Data collected 2006-2010. Altitude 300-600 m.a.s.l. Boreal temperate forest in the cold temperate climate zone with snow cover 3-6 months per year and varying snow

depths of 10-75 cm. Coniferous forest (taiga) is the dominant vegetation type and locally in the mountains are also tundra with only small plants in the form of dwarf trees and herbs. Norway spruce *(Picea abies)* and Scots pine *(Pinus sylvestris)* were the dominant tree species, and downy birch *(Betula pubescens)*, European white birch *(Betula pendula)*, and European aspen *(Populus tremula)* occurred in various mixtures. The limit to the tundra coincides basically with the tree line which is nearly 900 m altitude in the southern mountains. The climate is continental with temperatures ranging from 15°C in July and –7°C in January. Precipitation 600-800 mm/year 2005-2010 (Swedish Meteorological and Hydrological Institute). Resident species in most territories; moose *(Alces alces),* roe deer *(Capreolus capreolus),* Eurasian lynx *(Lynx lynx),* red fox *(Vulpes vulpes)*, badger *(Meles meles)*, European pine marten *(Martes martes),* European beaver *(Castor fiber),* European hare *(Lepus europaeus),* European jay *(Garrulus glandarius),* common raven *(Corvus corax)*, common buzzard *(Buteo buteo),* and white-tailed eagle *(Haliaeetus albicilla)*, hooded crow*(Corvux cornix)*, magpie *(Pica pica)* and in some territories brown bear *(Ursus arctos)*. Moose is the main prey for wolves all year round (Sand et al 2005, 2008) and therefore a potential source of carcasses for scavengers. In addition, humans are a large provider of moose carcass remains to scavengers mainly through hunter harvest but also through vehicle collisions.

IT: Alpe di Catenaia_(43-48°N, 11-43°E). Data collected 2010-2013. Altitude 490-1400 m.a.s.l. Camera monitoring of scavenging species was approved by Arezzo Province.
The study area is 120 km² and includes a small protected area of 27 km² in the centre where locked gates prevent public access by car. The climate is continental and is characterized by high humidity and rainfall. There is more than 80% forest cover with coppice, high trunk forests of Turkey oak (*Quercus cerris*) and chestnut (*Casanea sativa*) at lower elevation, and of beech (*Fagus sylvatica*) at upper ranges. Moreover conifers such as pine and black pine *(Pinus nigra)*, white spruce *(Abies alba)*, Douglas fir *(Pseudotsuga spp)* are interspersed into deciduous woods or form small patches of pure forests. Temperatures drop below freezing in winter with heavy snowfall occurring. Mean temperature 11.6 ° C (summer 17.5° C and winter 8° C). Precipitation was approx. 1000 mm/year. Resident species are roe deer, red fox, wild boar *(Sus scrofa)*, red deer *(Cervus elaphus),* fallow deer *(Dama dama),* European hare, pine marten, stone marten *(Martes foina)*, badger, wolf, crested porcupine *(Hystrix cristata)*, wildcat *(Felis sylvestris),* common buzzard, goshawk, sparrow hawk *(Accipiter nisus),* hooded crow and European jay. Wild boar is the main prey for wolves and cameras were located at mainly wild boar and roe deer carcasses. Human hunting harvest of wild boar was 5.89/km² and of roe deer 3.64/km² (Ståhlberg, unpublished results) and vehicle collisions was also a common cause of death.

Movement triggered camera systems
Movement-triggered cameras were placed at carcasses killed by wolves, remains from hunter harvest or ungulates killed in traffic collisions all year round (2006-2010). Cameras were set up when collared wolves where >2 km away from the carcass. Sites with remains from moose harvest were reported by hunters and cameras were set up the same day as shot. We used the cameras STC-WD1, STC-IR1 and STC-WD2-IR (85%) manufactured by Stealth Cam, (Grand prairie, Texas, USA), DvrEye™ Wireless PIR Model, DVR002, PixController Inc, (PA, USA), Multipir-12, Tecnofauna Ziboni s.r.l. (Rogno, Italy), Bushnell HD Trophy Cam, Bushnell Outdoor (KS, USA), BolyGuard 550M, Boly Media Communications Ltd (Shenzhen, China) and Uovision UM565 Uovsion Australia (Huntingdale VIC, Australia). Because red fox reacted to flash light used in camera brand STC-WD1, we removed the light and used only this type of camera during summer. Also, the light emitters were switched from camera brand STC-WD2-IR to emitters with longer wavelength creating invisible infrared light (LOKE Special Electronics, Skinnskatteberg, Sweden). Many mammal species also reacted to the visible infrared red light used in the DvrEye camera when taken during dark hours so we replaced them with the other brands. Cameras were programmed to shoot three photos when triggered by movement with a minimum of one minute between triggering events, or to take a sequence of video film, 20-60 seconds. Date and time were registered on each photo/film.

Cameras were placed on tree stems approximately 0.5-2.5 m above ground, depending on site location and terrain ruggedness (Sappington et al 2007) as well as risk of scavenger interference, 2-10 m from carcasses. The movement detectors were not triggered by birds smaller than jay or mammals smaller than bats. Date and time were registered on each photo/film. Camera sites were checked and memory cards and/or batteries changed every 1-6 week except for two cameras which used GPRS/MMS transmission and one of these had a solar cell panel as energy source.

All films and photos were visually analysed and categorised by camera id, video result, location, date, time, duration, species, number of individuals and behaviour (feeding, vigilant, looking at camera or other). The daily and nightly 24 hours activity at feeding sites were pooled in 6 time periods: 00:00-03:59, 04:00-07:59, 08:00-11:59, 12:00-15:59, 16:00-19:59, 20:00-23:59. Seasonal activity in SWE: *summer* May-September, *early winter* October-November, *mid-winter* December-February, *late winter* March-April and in IT: *summer* May-October, *early winter* November-December, *mid-winter* January-February, *late winter* March-April. Vegetation type, vegetation coverage, visibility, snow coverage and carcass data (consumption level at set up, cause of death, species, age, sex) were recorded at carcass sites. Coverage above carcass was estimated by visual determination of percentage of cover (vegetation or snow cover) in two categories (0-69% or 70-100%). Visibility of carcasses was estimated from the four cardinal points towards the carcass, by measuring the distance from where it could be detected. Visibility was then calculated as the average of all distances in the four directions and categorized as <15 m or ≥15 m. We defined a visiting occasion as recordings per individual with ≥11 minutes between films/photos.

Carcasses

Species, age, sex, cause of death and weight was recorded. The proportion of edible biomass consumed was visually estimated at the time of camera set up and each visit made to replace battery and memory card. Cameras were removed when carcasses were totally consumed or occasionally due to camera failure. Carcasses were moose, roe deer, wild boar and some fallow deer and red deer in different ages weighing 12-300 kg. Carcasses were reported from collared wolf data, hunters, the forestry service and the public. When found by roads, carcasses were relocated into the forest at undisturbed locations. In Alpe di Catenaia, local wild boar jaws, bones and hide provided from a veterinary study were used at a few sites. Since wolves are not GPS collared in Italy, we could not establish whether wolf-killed carcasses were hunted nor scavenged by resident or non-resident wolves.

Data analysis

When data was normally distributed, statistical significance was tested with single factor ANOVA and post-hoc Tukey HSD test. When not normally distributed, statistical significance was tested with the non-parametric Mann Whitney and Kruskal-Wallis test. Data was analysed using IBM SPSS Statistics 21.

Results

SWE: Cameras recorded at 67 carcasses/feeding sites between 0.42 and 10 days (mean 9.08 days per site), 24 hours/day, all year round from February 2006 to June 2010 (52 months). Cameras were triggered at 19,700 occasions whereof in 15,706 films/photos, scavenging species were identified and 561 unknown/unclear. 16 scavenging species were recorded at 67carcasses/feeding sites for 2916 days and nights. The most active scavenger was the red fox followed by common raven, pine marten, jay, goshawk, golden eagle, crow, wolf, magpie, badger, brown bear, domestic dog *(Canis familiaris)*, wild boar and only a few visits by eagle owl, sea eagle, wolverine and lynx. In 319 occasions (>11 min intervals) there were two or more individuals simultaneously. Vegetation type at camera sites were mainly spruce and Scots pine utilised in an intensively exploited forest industry with high vegetation coverage in 7.2%, medium 57% and low 35.8% respectively. Visibility at 44.9% of the carcasses/feeding sites was <15 m. At 39% of the camera sites, the recordings took place when there was no snow on ground, 20% when it was covered with 1-14 cm snow and 41% when covered with 15-55 cm. Carcasses were covered by >70% of snow in 27% of the visiting occasions. The most active

scavengers (individuals visiting occasions with ≥11 min intervals), were *Corvidae* spp. 48.4% followed by red fox 27.7%, birds of prey 11.1%, pine marten 8.3%, wolf 2.3%, brown bear 0.6%, dog 0.4%, wild boar 0.2%, lynx and wolverine 0.1% respectively.
IT: Cameras recorded at 137 carcasses/feeding sites between 4 and 291 days (mean 63 days per site), 24 hours/day, all year round from July 2010 to May 2013 (35 months). 11 species in 9,474 films/photos (9,294 films, 163 photos) and 263 hours of film were recorded for 5556 days and nights. The most visits were by the red fox followed by marten, then badger, dog, wolf, unknown, other species, wild boar, wildcat, bird of prey, *Corvidae* and polecat. In 3026 films there were two or more individuals simultaneously. Camera sites mainly consisted of beech or mixed forest with vegetation coverage; high 16.1%, medium 39.4% and low 44.6% respectively. Visibility at 54.8% of the carcasses/feeding sites was >15 m in at least three directions. At 73% of the camera sites, the recordings took place when there was no snow on ground, 18% when it was covered with snow and 9% temporarily with or without snow. Carcasses were never covered >70% with snow. The most active visitors were wild boar 44.4%, red fox 38.7%, marten 6.9%, dog 2.4% and wolf 2.4%.

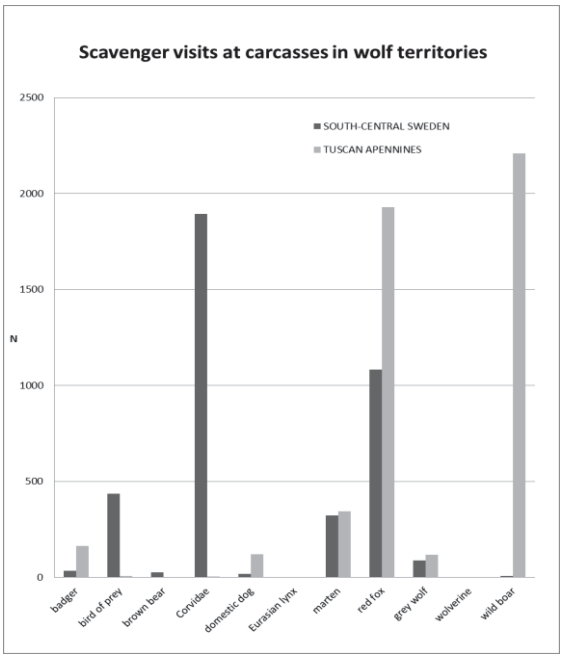

Fig. 1. Scavengers in wolf territories in South-central Sweden and the Tuscan Apennines, north-central Italy

Five common visiting species in south-central Sweden and the Tuscan Apennines
We compared individual visiting occasions of exclusively common mammalian scavenging species (red fox, marten, badger, wolf, wild boar) in SWE and IT, since avian scavenger visits were very rare in the latter area.

Within SWE and IT, Kruskal-Wallis test showed there was no significant difference in number of visiting occasions of the four species in SWE (H =0.14, n = 1076, 33, 318, 89, NS) or IT (H =6.95, n = 1843, 162, 346, 100, NS), but there was significant differences between the SWE species compared to the same specie in IT. Red fox differed between SWE and IT, a two-tailed Mann-Whitney exact test for two independent samples showed higher visiting occasions in IT than in SWE ($P < 0.0001$), as did marten ($P = 0.019$) and wolf ($P < 0.0001$). Badger showed no significant difference between SWE and IT being less frequent in the latter area.

Comparing each specie, there was a significant relationship between red fox in SWE and IT in 24 hour activity pattern: Spearman's $r_s = 0.886$, n = 6, $P = 0.019$, but seasonal pattern NS, badger 24 h: $r_s = 1.0$, n = 6, $P < 0.01$ but seasonal NA, marten 24h: $r_s = 0.9$, n = 6, $P = 0.037$ and seasonal NS, wolf 24 h NS and seasonal: r_s 4 = -0.949, n = 4, $P = 0.051$, wild boar 24 h NA and seasonal NS. There was no significant relationship of feeding site selection related to visibility, snow coverage or vegetation coverage within the species in SWE and IT.

Scavenger feeding site selection
SWE: Vegetation coverage was high in 7.2% of the camera sites, medium in 57.0% and low in 35.8% of the camera sites. 87.1% of all photos were taken when camera sites were covered with snow and 12.9% no snow. All avian scavengers clearly preferred

open areas with low vegetation and good visibility except for raven, jay and, particularly, sea eagle. Of mammal scavengers, brown bear and lynx preferred open areas but most noticeable was that pine marten appeared substantially in open areas with low vegetation. Badger and wolverine were always, and red fox most often, seen in dense vegetation with poor visibility. Sites with snow coverage was predominantly used by red fox and raven, but also wolf, badger and wolverine preferred high snow coverage. Wild boar and lynx never appeared at sites with snow cover. 20.9% of the cameras were <1 km from human disturbance and only red fox (1.2% of their total visits) and magpie (7.4% of their total visits) visited these sites.

IT: Vegetation type at camera sites were; mixed tree species 39%, beech 24%, spruce 8%, oak 5%, chestnut 1% and open areas with grass and shrub 23%. Vegetation coverage was high in 15.0%, medium in 40.5% and low in 44.5% of the camera sites. Wolves and badgers avoided open areas such as meadows and visited these areas in only 4.6% respectively 7.5% of their total visits. Avian scavengers and wolves preferred low vegetation and good visibility. Without snow coverage, red fox and wild boar appeared equally but when snow coverage at the site, red fox was the most active visitor. Avian scavengers seldom appeared when there was snow coverage and of mammals, nor did marten. 15.4% of the cameras were <1 km from human disturbance and avian scavengers appeared most of all with 100% of the *Corvidae* spp. visits, whilst red fox was the most common mammal with 39.2%. Disturbance by human activity is difficult to estimate for *Corvidae* spp. due to the low number of visits but the species often live close to human settlement where they can feed upon waste (Johnston 2001).

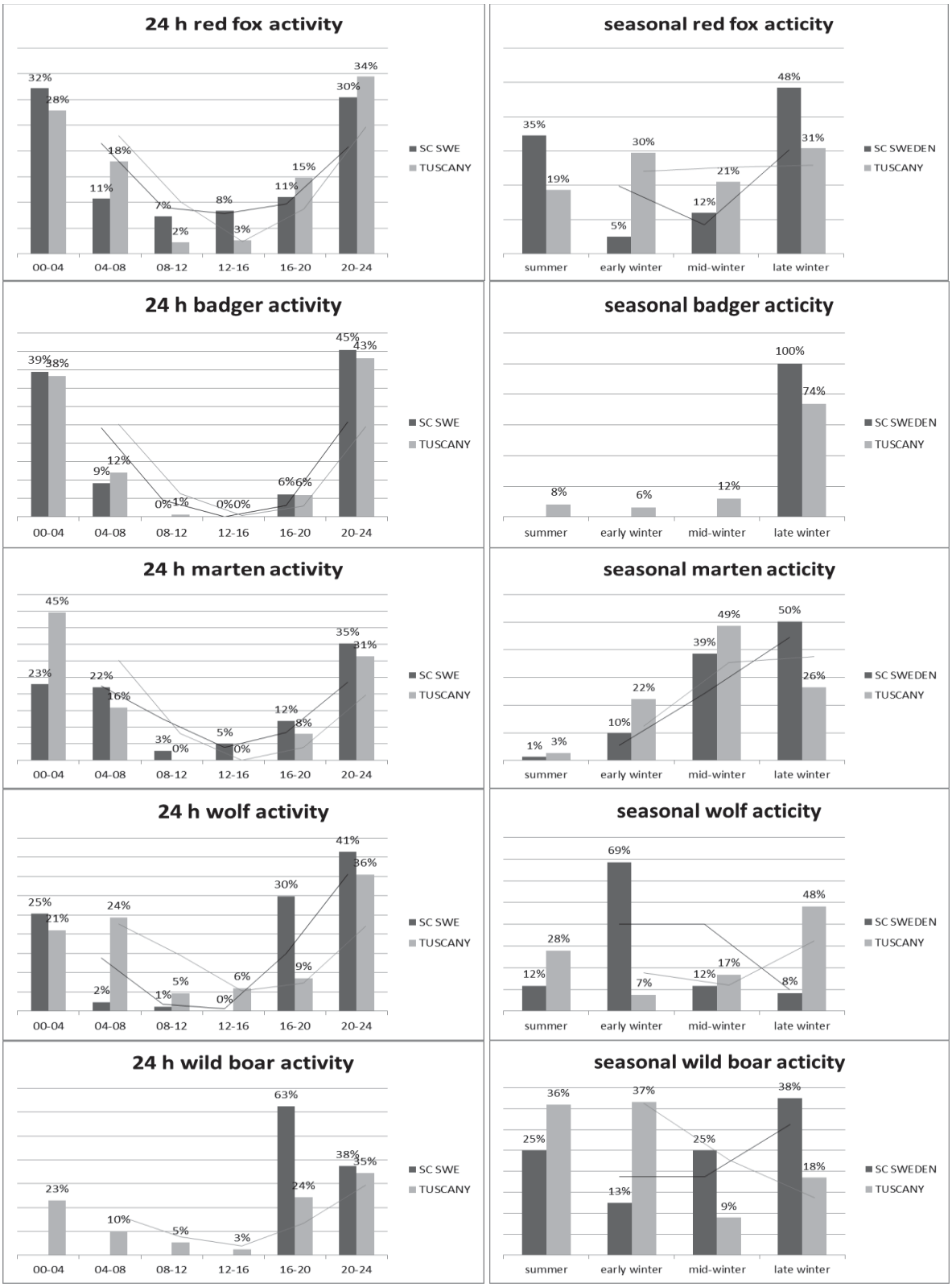

Fig. 2 The table show percentage of options but in statistic tests, sample N are used. Visibility from carcass in four directions (cardinal points), poor showing when at least two directions <15 m and good when at least three directions >15 m visibility. Vegetation coverage was observed from the carcass and classified as high when dense vegetation covered carcass, medium when some vegetation partly covered and low when open or only grass/shrub covered surrounding.

Tab.1. The table show percentage of options but in statistic tests, sample N are used. A Spearman's rank correlation coefficient is used and reports significant relationship between each specie in SWE and IT. 24 h activity at feeding site: 00:00-03:59, 04:00-07:59, 08:00-11:59, 12:00-15:59, 16:00-19:59, 20:00-23:59. Seasonal activity in SWE: *summer* May-September, *early winter* October-November, *mid-winter* December-February, *late winter* March-April and in IT: *summer* May-October, *early winter* November-December, *mid-winter* January-February, *late winter* March-April. Visibility from carcass in four directions (cardinal points), poor showing when at least two directions <15 m and good when at least three directions >15 m visibility. Vegetation coverage was observed from the carcass and classified as high when dense vegetation covered carcass, medium when some vegetation partly covered and low when open or only grass/shrub covered surrounding.

			red fox			**badger**			**marten**			**wolf**			**wild boar**		
		%	SWE	correlation	IT	SWE	correlation	IT	SWE	correlation	IT	SWE	correlation	IT	SWE	Correlation	IT
24 h	00-04		32,2		27,9	39,4		38,3	23,0		44,6	25,3		21,1			23,0
activity	04-08		10,7		18,0	9,1		12,0	22,0		15,9	2,3		24,3			10,2
	08-12		7,3	*P* = 0.019	2,2		*P* < 0.01	0,6	2,8	*P* = 0.037	0,1	1,1	NS	4,6		NA	5,4
	12-16		8,4		2,6				5,0					5,9			2,5
	16-20		11,1		14,8	6,1		6,0	11,9		8,0	29,9		8,6	62,5		24,3
	20-00		30,4		34,5	45,5		43,1	35,2		31,4	41,4		35,5	37,5		34,6
seasonal	summer		34,5		18,7			8,1	1,3		2,7	11,6		27,8	25,0		36,0
activity	early winter		5,0	NS	29,6		NA	6,3	9,7	NS	22,2	68,6	*P* = 0.051	7,4	12,5	NS	36,6
	mid-winter		12,0		21,0			11,9	38,7		48,7	11,6		16,7	25,0		9,0
	late winter		48,5		30,8	100,0		73,8	50,3		26,4	8,1		48,1	37,5		18,5
visibility	poor		73,6	NS	43,1	29,7	NS	59,9	47,7	NS	25,7	100	NS	25,7	60,0	NS	45,5
	good		26,4		56,9	70,3		40,1	52,4		74,3			74,3	40,0		54,5
snow coverage	no		54,7	NS	72,1	89,7	NS	93,6	92,3	NS	68,4		NS	57,3	99,1	NS	90,3
	yes		45,3		27,9	10,3		6,4	7,7		31,6	100		42,7	0,9		9,7
vegetation coverage	high		18,1	NS	17,6		NS	24,4	31,9	NS	20,5	1,1	NS	1,8		NS	13,5
	medim		47,5		34,1	0,5		25,0	43,3		33,8	97,5		35,8	32,5		45,8
	low		34,4		48,3	99,5		50,6	24,8		45,7	1,4		62,4	67,5		40,8

Discussion

Scavengers provide one of the most important yet underappreciated and poorly-studied ecosystem services. Our study of scavenging species in wolf territories in south-central Sweden and the Tuscan Apennines clearly showed that avian scavenging species dominates the former area and mammalian species the latter. The very few visits by avian scavengers in the Tuscan Apennines were unexpected and a potential explanation may be the carcass size. In Tuscany they were characterised by smaller size compared to the much larger in Sweden, were the wolf main prey is moose and not wild boar or roe deer. Many studies have shown that vegetation coverage may greatly influence where avian scavengers concentrate their food search (e.g. Getz 1961; Baker and Brooks 1981a) and can detect a large carcass more effectively from longer distances with their highly developed sight (Tucker 2000). Nonetheless, 29.6% of the feeding sites in south-central Sweden were open areas or had low vegetation coverage which was less than in the Tuscan Apennines with 45.2% of open areas. Another factor affecting the sight and detection ability is snow coverage (Formosov 1946), and the feeding sites in Sweden were covered with snow in 77.2% while the Tuscan Apennines 19.9%. When looking closer at bird of prey and corvids, the most common avian forest species are raven and jay which may increase when forest becomes fragmented and intermix with agricultural land offering additional food sources (Andrén 1992). Raven density in Sweden is ≈ 3 pairs/km^2 (Angelstam et al 1987) and jay ≈ 11 birds/km^2(Grahn 1990). The wolf territories, in which this camera study took place in, are all located in forests intermixed with agricultural land, therefore not a sustainable explanation of the low level of avian scavengers in TUS. Previous studies by Grahn (1990) and Patterson et al (1991) shows higher density of jay (11.4/km^2) in Maremma Natural Park, Tuscany, compared to southern Sweden during summer (11 jays/km^2) which was not consistent with the very few visits by jay in our study. However, Maremma Natural Park is located at the coast of western Tuscany, has a high agricultural component and is not in the Apennine mountain area in north-eastern Tuscany. Moreover, the wolf territories in south-central Sweden does not have as high level of agricultural landscape as in southernmost Sweden. Type of forestry practices have also been debated as increasing and decreasing raptor populations (Widén 1994; Petty 1999), nonetheless, the highly exploited forestry industry in Sweden with frequent clear-cuts should be less attractive for avian scavengers such as raven and jay compared to the re-foresting process of the landscape in Apennines. Tornberg et al (2006) found in a review of the Northern goshawk on average 3 pairs/km^2 in Fennoscandia since the 1950s and Penteriani and Faivre (1997) did a 10-year long study of Mediterranean goshawks showing a strongly lower density of 5.03 pairs/100 km^2 in the Abruzzo Apennines, central Italy (approx. 300 km south of TUS). A further explanation can be found in the strong propensity of carrion crow in Italy to rely on human generated food sources: this was the main cause of their increase in the country and make these birds more common close to human settlements than anywhere else. The same can be true for other Corvidae species like magpie and jays that are more common in agricultural landscape often controlled by wildlife authorities, rather than in mountains in Central Italy. Other threats to avian scavengers are lead poisoning when consuming game mammal carrion shown in Germany (Nadjafzadeh et al 2012) which was not investigated in our two study areas but an interesting question for future research.

Habitat features influences scavenging species feeding behaviour (Hunter et al 2007), however, air temperature exceeding 17ºC has probably the strongest effect on carcass fate as insects and arthropods will rapidly speed up decomposition (DeVault et al 2004). The longer summer period with higher temperatures in the Tuscan Apennines contributed to faster decomposition, but also of scavenging behaviour clearly shown in wild boar. Wild boars selected the rich supply of insects and arthropods during the warm period and the access to food items not covered by snow was easy during the cold period, suggesting that there was not as high demand for alternative and supplementary food sources as seen in south-central Sweden. The few occasions when wild boar scavenged in the Tuscan Apennines, carcasses could also be wild boar (confirming cannibalism). Animal carcasses are not an attractive food source for carnivores and omnivores living in or near human habitats where there are other abundant food sources, such as rubbish dumps and domestic animals (Pozio 1998). Tuscany has considerably higher

human density than south-central Sweden but the Apennine ecosystem is changing in recent decades due to abandonment of traditional farming and forest activities which increases forest coverage benefitting wildlife. However, the few visits by avian scavengers may indicate that this mountainous habitat is not strongly selected by birds of prey or Corvidae spp.

Daily (24 hour) and seasonal partitioning

There are several levels in a scavenger guild where smaller members and supposedly less competitive species adopt strategies such as changes in their spatial or temporal foraging patterns to reduce interferences (Arjo and Pletscher 1999). The daily partitioning of feeding sites in south-central Sweden was basically divided between avian scavengers during day and mammalian scavengers during night. In the Tuscan Apennines, the 24 hour partitioning was rather straight forward with mainly nocturnal activity without any clear avoidance between the mammalian scavenging species, only different peak hours. However, one must take into account that hours of light differ with latitude and that this should be acknowledged when comparing activity in these two areas. Sweden has more light per 24 hours during the summer season and less during the winter season compared to Italy, which can bias the result when classifying equivalently. Red fox has its peak activity before midnight whilst martens have it after midnight. Seasonal partitioning in south-central Sweden was not seen in the main scavenger species raven and red fox, they actually followed the same yearly pattern. However, in the Tuscan Apennines, in mid-winter when red fox are less active, martens have the highest activity and there is a clear season-temporal partitioning.

Feeding site selection

We never recorded any intra-guild predation or attacks causing injury at the feeding sites, nevertheless, a few occasions when red fox chased away martens. Scavenging individuals were alert and detected approaching intra-guild members. Scavengers who avoid feeding sites frequently used by wolf and red fox may do this as an anti-predator strategy. Good visibility and low vegetation coverage was not important in Swedish wolves, but rather important for the Tuscan wolves. Red fox selected poor visibility with high vegetation in Sweden but somewhat the opposite in Tuscany. Only lynx and pine marten in Sweden and wildcat, and martens in Tuscany chose poor visibility and high vegetation. Noticeable is the pine marten who chooses the same sites as red fox in Sweden. Both species follow a similar daily and seasonal activity pattern in SWE as showed in previous studies (Wikenros et al, unpublished), however habitat characteristics may be a more crucial factor. Red fox in IT chose feeding sites with good visibility and open areas more often than did marten (40.1 and 13.8% respectively) but also in a larger perspective; snow coverage was more accepted by fox than by marten (Tab.1).

The four common scavenging species

The common scavenging mammalian species red fox, badger, marten and wolf all shows a delayed daily activity pattern in IT compared to SWE when looking simply at time. All four species showed lower activity around mid-day in both SWE and IT. Seasonal differences in red fox activity may be explained by the large portion of berries during autumn. There was also a quite low number of visits by badgers in SWE and all occurred in late winter as did most of the visits in IT. This may be explained by their preference of earth worms (Goszczynski et al 2000) which are not as accessible as the earth crust is frozen during late winter, particularly in SWE. Marten has a similar pattern except for in late winter when IT shows much less scavenging, most likely due to earlier spring and reproduction period when shift to other food resources (Wikenros et al, unpublished). Previous studies have shown nocturnal wolf activity in southern Europe (Vilà et al 1995; Ciucci et al 1997) due to centuries of persecution, but the spatial and temporal avoidance of man is an adaptation in each geographic region (Kaartinen et al 2005; Theuerkauf et al 2003c; Theuerkauf et al 2007). The most apparent difference when comparing wolf activity (Fig. 2) is the higher activity in the late afternoon-early evening in south-central Sweden and the morning 04:00-08:00 in the Tuscan Apennines. The activity peak was the same; evening before midnight. The resting period begins and ends earlier in northern European climate conditions. Seasonal

differences were shown by early winter being the absolute peak of wolf scavenging in south-central Sweden, while a more moderate peak was shown in late winter by the Tuscan Apennine wolves. Increased scavenging in early winter may be correlated to the human hunting season as removal of large moose carcasses in SWE is not as sufficient as small carcasses such as wild boar and roe deer in IT. Moreover, the lowest scavenging activity in south-central Sweden was seen in late winter which may indicate that the Swedish wolves are not typical scavengers. However, grey wolf is an adaptable predator and consequently a facultative scavenger who changes food source when opportunity is given. As seen in a diet study from Tuscany (Ståhlberg, unpublished), lower scavenging in early to mid-winter in the Tuscan Apennines, may be the result of wild boar juveniles being easy to catch due to lack of anti-predator behaviour and experience. Hunting a 10-35 kg prey animal with low risk of injury may be preferred instead of scavenging during that time period, however, the Tuscan wolves followed the common scavenging patter with the peak in late winter.

Conclusively, we can summarise this study with the virtually absence of avian scavengers in the Tuscan Apennines, the similar but somewhat delayed daily activity pattern and a very non-correlated seasonal pattern. Only badger followed the typical scavenger pattern of utilising carrion as in alternative food resource in late winter in both areas. Red fox, marten and wild boar also showed this behaviour in SWE which may indicate that scavenging in colder climates, is a more important type of nutritional attainment, than in warmer climates.

Acknowledgement

We thank all people who through the years helped setting and checking cameras. The study was funded by Axel and Margaret Ax:on Johnsons Foundation and Helge Ax:on Johnsons Foundation.

References

Wilson, E.E. and Wolkovich, E.M. 2011. Scavenging: how carnivores and carrion structure communities. Trends in Ecology and Evolution, 26:129-135.

Andrén, H. 1992. Corvid density and nest predation in relation to forest fragmentation: A landscape perspective. Ecology, 73:794-804.

Angelstam, P., Lindström, E. and Widen, P. 1984. Role of predation in short-term population fluctuations of some birds and mammals in Fennoscandia. Oecologia (Berlin) 62:199-208.

Arjo, W.M., Pletscher, D.H., 1999. Behavioral responses of coyotes to wolf recolonization in northwestwern Montana. Canadian Journal of Zooogy. 12, 1919–1927.

Atwood, T. C. and Gese, E.M. 2008. Coyotes *(Canis latrans)* and recolonizing wolves *(Canis lupus)*: social rank mediates risk conditional behaviour at ungulate carcasses. Animal Behaviour, 75:753–762.

Baker, J. A. and Brooks, R. J. 1981a. Distribution patterns of raptors in relation to density of Meadow Voles. Condor 83: 42-47.

Berger, K.M. and Gese, E.M. 2007. Does interference competition with wolves limit the distribution and abundance of coyotes? Journal of Animal Ecology, 76:1075-1085.

Bergerud, A.T. 1980. A review of the population dynamics of caribou and wild reindeer in North America. *In:* E. Reimers, E. Gaare, S. Skjennebeg (eds). *Proceedings of the 2nd International Reindeer/caribou Symposium, Røros, Norway*. pp 556-581.

Blazquez, M., Sanchez-Zapata, J.A., Botella, F., Carrete, M., Eguía, S. 2009. Spatio-temporal segregation of facultative avian

scavengers at ungulate carcasses. Acta Oecologica-International Journal of Ecology 35:645-650.

Ciucci, P., Boitani, L., Pelliccioni, E.R., Rocco, M., Guy, I. 1996. A comparison of scat analysis methods to access the diet of the wolf *Canis lupus*. Wildlife Biology, 2:37-48.

De Vault, T.L., Brisbin, L. Jr., Rhodes, O.E. Jr. 2004. Factors influencing the acquisition of rodent carrion by vertebrate scavengers and decomposers. Canadian Journal of Zoology, 82:502-509.

DeVault, T.L., Olin E. Rhodes, O.E., Shivik, J. A. 2003. Scavenging by Vertebrates: Behavioral, Ecological, and Evolutionary Perspectives on an Important Energy Transfer Pathway in Terrestrial Ecosystems. Oikos, 102:225-234.

Formosov, A. N. 1946. The snow cover as an environmental factor and its importance in the life of mammals and birds. - Occ. Publ. No. 1, Boreal Institute, University of Alberta.

Frelich, L.E. 2002. Forest dynamics and disturbance regimes: studies from temperate evergreen-deciduous forests. New York: Cambridge University Press.

Getz, L. L. 1961. Hunting areas of the Long-eared Owl. Wilson Bull. 73: 79-82.

Goszczynski, J., Jedrzejewska, B., Jedrzejewski, W. 2000. Diet composition of badger *(Meles meles)* in a pristine forest and rural habitats of Poland compared to other European populations. Journal of Zoology (London), 250:495-505.

Grahn, M. 1990. Seasonal Changes in Ranging Behaviour and Territoriality in the European Jay *Garrulus g. Glandarius*. Ornis Scandinavica, 21:195-201.

Green, I.G., Mattson, D.J., Peek, J.M. 1997. Spring feeding on ungulate carcasses by Grizzly bears in Yellowstone National Park. The Journal of Wildlife Management. 61:1040-1055.

Houston, D.C. 1979. The adaptions if scavengers. In: Sinclair, A.R.E. and Griffiths, M.N. (Eds.) *Serengeti, dynamics of an ecosystem.* P. 263-286. Chicago: The University of Chicago Press.

Hunter, J. S., Durant, S. M., Caro, T. M. 2007. To flee or not to flee: predator avoidance by cheetahs at kills. Behavioural Ecology and Sociobiology, 61:1033–1042.

Jennelle, C.S., Samuel, M.D., Nolden, C.A., Berkley, E.A. 2009. Deer carcass decomposition and potential scavenger exposure to chronic wasting disease. Journal of Wildlife Management, 73:655-662.

Johnston, R.F. 2001. The synanthropic birds of North America. J.M. Marzluff, R. Bowman, R. Donnelly (Eds.), Avian Ecology and Conservation in an Urbanizing World, Kluwer Academic, Norwell, MA, pp. 49–67.

Kaartinen, S., Kojola, I. & Colpaert, A. 2005: Finnish wolves avoid roads and settlements. Annales Zoolici Fennici, 42:523-532.

Lindström, E.R., Brainerd, S.M., Helldin, J.O., Overskaug, K. 1995. Pine marten - red fox interactions: a case of intraguild predation? Annales Zoologici Fennici 32: 123–130.

Macdonald, D. W., Buesching, C. D., Stopka, P., Henderson, J., Ellwood, S. A., Baker, S. E. 2004. Encounters between two sympatric carnivores: red foxes *(Vulpes vulpes)* and European badgers *(Meles meles)*. Journal of Zoology, 263:385–392.

Magoun, A.J. 1976. Summer scavenging activity in north-eastern Alaska. M.S. thesis, University of Alaska, Fairbanks, AK, USA.

Mattisson, J., Persson, J., Andrén, H., and Segerström, P. 2011. Temporal and spatial interactions between and obligate predator, the Eurasian lynx (*Lynx lynx*), and a facultative scavenger, the wolverine (*Gulo gulo*). Cananadian Journal of Zoology, 89: 79–89.

May, R., van Dijk, J., Wabakken, P., Swenson, J.E., Linnell, J.D.C., Zimmermann, B., Odden, J., Pedersen, H.C., Andersen, R., Landa, A. 2008. Habitat differentiation within the large-carnivore community of Norway's multiple-use landscapes. Journal of Applied Ecology, 45:1382–1391.

Merkle, J.A., Stahler, D.R., Smith, D.W. 2009. Interference competition between gray wolves and coyotes in Yellowstone National Park. Canadian Journal of Zoology, 87:56-63.

Nadjafzadeh, M., Hoper, H., Krone, O. 2012. The link between feeding ecology and lead poisoning in White-tailed Eagles. The Journal of Wildlife Management, 77:48-57.

Patterson, I.J., Cavallini, P., Rolando, A. Density, range size and diet of the European ay *Garrulus glandarius* in the Maremma Natural Park, Tuscany, Italy, in summer and autumn. Ornis Scandinavica, 22:79-87.

Penteriani, V. & Faivre, B. 1997. Breeding density and nest site selection in a Goshawk *Accipiter gentilis* population of the Central Apennines (Abruzzo, Italy), Bird Study, 44:2, 136-145.

Petty, S.J. 1999. Diet of tawny owls *(Strix aluco)* in relation to field vole *(Microtus agrestis)* abundance in a conifer forest in northern England. Journal of Zoology, 248:451–465.

Pozio, E. 1998. Trichinellosis in the European Union: Epidemiology, ecology and economic impact. Parasitology Today, 14:35-38.

Putman, R.J. 1983. Carrion and dung: the decomposition of animal wastes. The Institute of Biology's Studies in Biology no. 165. Edward Arnold Ltd, London.

Sappington, J.M, Longshore, K.M., Thompson, D.B. 2007. Quantifying landscape ruggedness for animal habitat analysis: A case study using bighorn sheep in the Mojave Desert. Journal of Wildlife Management, 71:1419-1426.

Selva, N. and Fortuna M.A. 2007. The nested structure of a scavenger community. Proceedings of the Royal Society B 274: 1101–1108.

Theuerkauf, J., Gula, R., Pirga, B., Tsunoda, H., Eggermann, J., Brzezowska, B., Rouys, S. & Radler, S. 2007. Human impact on wolf activity in the Bieszczady Mountains, SE Poland. Annale Zoologici Fennici. 44, 225—231.

Theuerkauf, J., Jedzejewski, W., Schmidt, K., Okarma, H., Ruczynski, I., S´niezko, S. & Gula, R. 2003c. Daily patterns and duration of wolf activity in the Białowieza Forest, Poland. Journal of Mammalogy. 84, 243—253.

Tornberg, R., Korpimaki, E., Jungell, S., Reif, V. 2006. Delayed numerical response of goshawks to population fluctuations of forest grouse. Oikos, 113:572-572.

Travaini, A., Donázar, J.A., Rodríguez, A., Ceballos, O., Funes, M., Delibes, M., Hiraldo, F. 1998. Use of European hare *(Lepus europaeus)* carcasses by an avian scavenging assemblage in Patagonia, 246:175-181.

Tucker, V.A. 2000. The deep fovea, sideways vision and spiral flight paths in raptors. Journal of Experimental Biology. 203:3745-3754.

Widén, P. 1994. Habitat quality for raptors: a field experiment. Journal of Avian Biology, 25: 219-223.

Wikenros, C., Sand, H., Ahlqvist, P., Liberg, O. 2013. Biomass flow and scavengers use of carcasses after re-colonization of an apex predator. PLOS ONE 8 (10) e77373.

Vilà, C., I., Amorim, I.R., Leonard, J.A., Posada, D., Castroviejo, J., Petrucci-Fonseca, F., Crandall, K.A., Ellegren H. and Wayne, R.K. 1999. Mitochondrial DNA phylogeography and population history of the grey wolf *Canis lupus*. Molecular Ecology, 8:2089–2103.

Wilmers, C.C., Crabtree, R.L., Smith, D.W., Murphy, K.M., Getz W.M. 2003. Trophic facilitation by introduced top predators: grey wolf subsidies to scavengers in Yellowstone National Park. Journal of Animal Ecology 72: 909–916.

PAPER IV

The function of vigilance in sympatric facultative scavengers in an Apennine wolf territory

SOPHIE STÅHLBERG AND MARCO APOLLONIO

Department of Natural and Environmental Science, University of Sassari, Via Muroni 25, Sassari 07100, Sassari, Italy.

Abstract:
Scavenging guilds in apex predator habitats often has several trophic levels with varying intra-guild predation, competition and interaction. Apex predators can control subordinate predators by limiting their numbers and affecting behaviour but also supply a continuous food source by abandoning carcasses. The scavenger guild in Alpe di Catenaia was monitored by a movement triggered camera system for three years to determine intraguild predation and the behaviour response in the subordinate scavengers. Wild boar visited most feeding sites but only scavenged in 1.4% of their visits as they fed on insects and arthropods around the carcasses. Red fox was the dominant scavenger and showed clearly the highest vigilance behaviour while the martens fed more per visiting occasion. In spite of being the smallest scavenger, martens appeared within the shortest time after other scavenging species had left the site. Although there are low numbers of birds of prey in the Tuscan Apennines, foxes commonly looked upwards to the tree canopy and sky. Badger showed merely any vigilance, did not feed much on carcasses but exceedingly scent-marked. Wolves showed highest vigilance in relation to feeding at carcasses among the scavengers. Sites with low vegetation coverage with good visibility was selected by all scavengers except martens who selected poor visibility and low moon illumination. Most scavengers were nocturnal, showed weak response to twilight hours or moon illumination and all but red fox avoided human disturbance areas.

Key words: vigilance, intraguild, competition, anti-predator behaviour, scavenging

Introduction

An optimal foraging theory is used to determine a consumer's actual diet within its wide potential range, and balance the pros and cons so as to maximise its overall rate of energy intake (MacArthur & Pianka 1966). Predation by top predators on intermediate predators may not only reduce competition through a numerical effect on the intermediate predators, but should also lead to a change in behaviour with an increased vigilance of the targeted species (Kimbrell et al. 2007). A successful strategy maximises feeding rate while minimising the risk of predation and in some mammals, habitat shifts result in reduced foraging opportunities (Sih 1980; Lima & Dill 1990). Predators should concentrate their search effort on those patches yielding greatest net gain of energy, although other factors, such as nutrient constraints and predation risk, may also influence the foraging decisions (Tinbergen 1981) and large carnivores play an important role maintaining balance in all trophic levels in terrestrial ecosystems (Hebblewhite et al 2005; Beschta & Ripple 2009). Several approaches, from direct lethal predation to indirect behavioural effects that alter prey distribution and habitat selection by intraguild members and prey species, are utilised by top predators (Lima & Dill 1990;

Berger et al 2008; Kittle et al 2008). Keystone species, such as the grey wolf, are however not only a predation risk for intermediate predators, they also abandon incompletely consumed carcasses for scavenging species. As top predators, they are not dependent on winter carrion and thereby not attracted to carcass sites, hence other mesopredators such as red fox, may have less interference competition with wolves and higher presence at carcass sites (Linell & Strand 2000). Scavenging species may choose several food recourses with temporal-, spatial- and cost dependant variances (Ståhlberg et al, unpublished), carrion being most available in late winter when many herbivore species suffer from food shortage, weakness and starvation. It has been suggested that smaller, subdominant species coexist with their larger and more dominant counterparts through temporal partitioning of habitats and resources (Pianka 1974, Schoener 1974a, Durant 1998, Linnell and Strand 2000, Harrington et al. 2009). Members of a scavenger guild can follow others to new feeding sites and even feed on carcasses simultaneously (Macdonald et al 2004; Wikenros et al, unpublished).

The risk allocation hypothesis predicts that prey is expected to adjust key anti-predator behaviours such as vigilance to tempo-spatial variation in risk and the objectives with this study was to establish how vigilance is used as an anti-predator investment by scavengers in Tuscan Apennine wolf territories. We hypothesise that level of vigilance is a measurement of a species trophic level in a scavenger guild and predict that (1) scavenger body size is an important factor regulating level of vigilance, (2) larger scavengers benefit by following smaller scavengers to feeding sites, and (3) the low number of avian predators in the Tuscan Apennines results in less vigilance than scavengers in Swedish wolf territories where there is a higher abundance of birds of prey. To test this, we will look at scavenger guild member numbers, behaviour at carcasses/feeding sites, site selection, and other possible factors affecting vigilant behaviour such as distance to human disturbance, diurnal-nocturnal activity and the lunar cycle.

Material and methods

Study area

Alpe di Catenaia (43-48°N, 11-43°E). Data collected July 2010 – May 2013. Altitude 490-1400 m.a.s.l. Camera monitoring of scavenging species was approved by Arezzo Province.

The study area is 120 km² and includes a small protected area of 27 km² in the centre where locked gates prevent public access by car. The climate is continental and is characterized by high humidity. There is more than 80% forest cover with coppice, high trunk forests of Turkey oak (*Quercus cerris*) and chestnut (*Casanea sativa*) at lower elevation, and of beech (*Fagus sylvatica*) at upper ranges. Moreover conifers such as pine and black pine *(Pinus negra)*, white spruce *(Abies alba)*, Douglas fir *(Pseudotsuga spp)* are interspersed into deciduous woods or form small patches of pure forests. Temperatures drop below freezing in winter with heavy snowfall occurring. Mean temperature 11.6 ° C (summer 17.5° C and winter 8° C). Precipitation was approx. 1000-1600 mm/year. Resident species are roe deer *(Capreolus capreolus),* red fox *(Vulpes vulpes)*, wild boar *(Sus scrofa)*, red deer *(Cervus elaphus),* fallow deer *(Dama dama),* European hare *(Lepus Europaeus),* pine marten *(Martes martes),* stone marten *(Martes foina)*, European badger (*Meles meles)*, wolf *(Canis lupus)*, crested porcupine *(Hystrix cristata)*, wildcat *(Felis sylvestris),* common buzzard *(Buteo buteo),* goshawk *(Accipiter gentilis)*, sparrow hawk *(Accipiter nisus),* hooded crow *(Corvux cornix)* and European jay *(Garrulus glandarius).*

Movement triggered camera systems

Movement-triggered camera systems were placed at carcasses killed by wolves or death of other causes year round. Wild boar is the main prey for wolves (Davis et al 2012; Ståhlberg et al Chapter II) and cameras were located at mainly

wild boar and roe deer carcasses. Five different camera systems were used: DVREye™ Wireless PIR Model, DVR002, PixController Inc, (PA, USA), Multipir-12, Tecnofauna Ziboni s.r.l. (Rogno, Italy), Bushnell HD Trophy Cam, Bushnell Outdoor (KS, USA), BolyGuard 550M, Boly Media Communications Ltd (Shenzhen, China) and Uovision UM565 Uovsion Australia (Huntingdale VIC, Australia). Cameras were programmed to take a sequence of video film or in a few cases, 1-3 photos per second with one second of interval (BolyGuard 550M) when triggered by movement. Cameras were placed between 0.5-2 m above the ground on tree stems, depending on site location and terrain ruggedness (Sappington et al 2005) as well as risk of scavenger interference, 2-10 m from carcasses. The movement detectors were not triggered by smaller scavenging birds then jays or mammals than bats. Date and time were stamped on every film/photo. Many mammal species reacted to the visible infrared red light used in the DVREye camera when taken during dark hours so we replaced them with the other four brands. Camera sites were checked and memory cards and/or batteries changed every 2-6 week except for two cameras which used GPRS/MMS transmission and one of these had a solar cell panel as energy source.

Carcasses

Species, age, sex, cause of death and weight was recorded. Visits to cameras were made between 7-21 days to replace battery and memory card. Cameras were removed when carcasses were totally consumed or occasionally due to camera failure. 38 carcasses were utilised in the study, mainly roe deer followed by wild boar and some fallow deer and red deer. Cause of death of the carcasses was primarily traffic killed followed by hunting injuries, wolf predation, natural or unknown reasons. 27 of the carcasses were adults, 3 sub adults and 6 juvenile, weighing 12-49 kg. Carcasses were reported from the forestry service and the public and when found by roads, carcasses were relocated into the forest at undisturbed locations. Since wolves were not GPS collared, we could not establish whether wolf-killed carcasses were hunted nor scavenged by resident or non-resident wolves.

Data analysis

All films and photos were visually analysed and categorised by camera id, video result (activity), location, date, time, duration, species, number of individuals and behaviour. As scavengers, once arrived to the carcass, very rarely left the site for more than 10 minutes during a longer stay (Ståhlberg et al, unpublished), we classified a visiting occasion when there was ≥11 minutes between two feeding bouts. For establishing guild member interactions or interference, we looked at a specie who visited a feeding site where another specie had been 0-180 minutes earlier. Behaviour was defined as: *Feeding* - chewing, *Vigilant* - a head lift which interrupts feeding activity on the carcass, followed by visual scanning of the environment (Quenette 1990), *Looking upwards* - raising head and looking toward the tree canopy or sky, *Scent-marking* - urinating, excavating or rubbing side of head and/or neck on ground or vegetation, *Looking at camera* - eyes focusing directly on the camera, *Other* - inspecting, searching, social interaction (mainly wild boar and fox), moving, grooming (mainly fox and marten). Each behaviour and proportion was then tested against the other scavenger guild members. The daily and nightly 24 hours activity at feeding sites were pooled in 6 time periods: 00:00-03:59, 04:00-07:59, 08:00-11:59, 12:00-15:59, 16:00-19:59, 20:00-23:59. Seasonal activity: *summer* May-October, *early winter* November-December, *mid-winter* January-February, *late winter* March-April. Coverage above carcass was estimated by visual determination of percentage of cover in two categories (0-69% or 70-100%). Visibility sideways of carcasses was estimated from the four cardinal points, by measuring the distance from where it could be detected. Visibility was then calculated as the average of all distances in the four directions and categorized as 0-14 m (poor) or ≥15 m (good). Camera sites located < 1 km from farms, forestry service or other human activity were used to evaluate the effect of human disturbance. Visits during light or dark hours, as well dawn and dusk were recorded. Crepuscular periods were classified as the morning twilight starting 30 min before sunrise and the evening twilight starting at sunset and ending 30 min after. Nocturnal visits at full moon and new moon +/- 72 h were recorded. When data was normally distributed, statistical

significance was tested with single factor ANOVA and post-hoc Tukey HSD test. When not normally distributed, statistical significance was tested with the non-parametric Mann Whitney and Kruskal-Wallis test. Data was analysed using IBM SPSS Statistics 21.

Results

Cameras recorded at 137 carcasses/feeding sites between 4 and 291 days (mean 63 days per site), 24 hours/day, all year round from July 2010 to May 2013 (35 months). Over 17 species in 10,085 films/photos (9,922 films, 163 photos) with 263 hours of film were recorded for 5556 days and nights. In 3026 films there were two or more individuals simultaneously. Camera sites mainly consisted of beech or mixed forest with vegetation coverage; high 16.1%, medium 39.4% and low 44.6% respectively. Visibility at 54.8% of the carcasses/feeding sites was >15 m in at least three cardinal point directions. At 73% of the camera sites, the recordings took place when there was no snow on ground, 18% when it was covered with snow and 9% temporarily with or without snow. Totally 5366 visiting occasions were calculated whereof scavengers; wild boar 38.2%,red fox 34.5%, marten 6.1%, badger 2.8%, domestic dog *(Canis familiaris)* 1.9%, wolf 1.6%, *Corvidae* spp. 0.09%, bird of prey 0.09%,

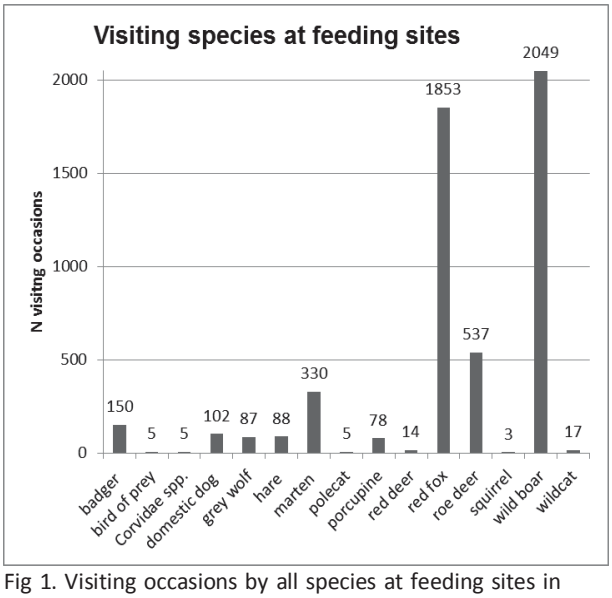

Fig 1. Visiting occasions by all species at feeding sites in Alpe di Catenaia 2010-2013.

polecat *(Mustela putorius)* 0.09% and non-scavengers; porcupine 1.5%, wildcat 0.3%, roe deer 10%, red deer 0.3%, hare 1.6% and red squirrel *(Sciurus vulgaris)* 0.03%. Wild boar fed on the carcass itself in only 1.4% of their visits, the major part of their feeding was on insects and arthropods around the carcass (Ståhlberg, unpublished). Domestic dog visited mainly daytime during autumn and winter when wild boar hunting season took place. However, there were some escaped or free roaming dogs which consumed entire carcasses at least at two occasions. Birds of prey and corvids were very rare (Ståhlberg, unpublished). It was visually impossible to distinguish between pine marten and stone marten why both were classified as 'marten'.

Scavenger guild members interaction or interference

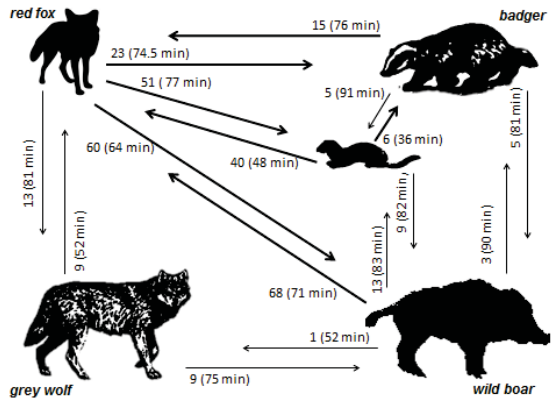

Fig 2. Number of observations when scavengers follow other scavengers and average minutes after the previous visitor has left the carcass/feeding site.

Two or more individuals of different species visited the sites simultaneously in only five occasions with fox and wild boar, twice with fox and marten and once with fox and wolf. Marten and fox withdrew immediately when the superior scavenger appeared but fox and wild boar did not react noticeably upon each other. The highest interaction between the most common scavenging (thus excluding wild boar) species– red fox, badger, marten, wolf, were between red fox and marten seen in Figure 2. Foxes followed marten at 51 occasions, between 0-168 min after marten had left (average 77

Fig 3. Behaviours at feeding sites were defined as *Feeding* - chewing, *Vigilant* - a head lift which interrupts feeding activity on the carcass, followed by visual scanning of the environment, *Looking upwards* - raising head toward tree canopy or sky, *Scent-marking* - urinating, excavating or rubbing side of head and/or neck on ground or vegetation, *Looking at camera* - eyes focusing directly on the camera, *Other* - inspecting, searching, social interaction (mostly wild boar and fox), moving, grooming (only fox and marten). Percentage of activity or state at visits to carcasses/feeding sites. Human disturbance <1 km from farms, forestry service or other human activity, behaviour, full moon and new moon +/- 72 h, diurnal and nocturnal visits or crepuscular activity at sunrise - 30 min and sunset +30

	visits	**human disturbance**	**behaviour at carcass**						**lunar cycle**		**dirunal**	**crepuscular**		**nocturnal**
	N	*< 1 km*	*feeding*	*vigilance*	*other*	*looking at camera*	*looking upwards*	*scent-marking*	*full moon*	*new moon*	*light*	*dawn*	*dusk*	*dark*
badger *Meles meles*	150	10,4	10,2	1,2	96,4	1,8		22,6	17,4	24,0	6,7			93,3
birds of prey	5	28,6							20,0	20,0	75,0			25,0
Corvidae spp.	5	100,0									80,0	20,0		
domestic dog *Canis familiaris*	102													
grey wolf *Canis lupus*	87	11,9	11,1	17,6	88,2	11,8		2	21,1	15,8	11	8,2		80,8
hare *Lepus europaeus*	88								23,5	18,4				
marten *M. martes, M.foina*	330	17,8	57,3	15,9	70,5	8,9	0,7	1,5	14,5	27,6				100
polecat *Mustela putorius*	5													
porcupine *Hystrix cristata*	78	20,9							15,8	20			3,4	96,6
red deer *Cervus elaphus*	14								28,6	7,1	66,7			33,3
red fox *Vulpes vulpes*	1853	39,2	47,6	42	64,1	21,6	3,1	3,8	28,9	23,9	4,4	1,4	1	93,2
red squirrel *Sciurus vulgaris*	3													
roe deer *Capreolus capreolus*	537								22,4	17,7	60	4,3	6,7	29,1
wild boar *Sus scrofa*	2049	24,7	2,9	16,1	96,6	10,8			28,5	21,0	3,9	1,4	0,7	94
wildcat *Felis sylvestris*	17	29,4												
other	43													

min), but martens followed fox in 40 occasions, from 0-134 min (average 48 min) which in a Mann-Whitney test, is significantly closer to when the fox has left the site than vice versa: $U = 761.5$, $n = 51, 40$, $P = 0.039$. Also tested; badger followed fox ($n = 15$, average 76 min), fox followed badger ($n = 23$, average 74.5 min), marten followed badger ($n = 6$, average 36 min), badger followed marten ($n = 5$, average 91 min), wolf followed fox ($n = 9$, average 52 min), fox followed wolf ($n = 13$, average 81 min) and wolf followed wild boar ($n = 6$, average 61 min) but all of these were NS.

Behaviour at feeding site

A Kruskal-Wallis test shows significant difference in scavenger behaviour at feeding sites: $H = 11.96$, $n = 8072, 214, 1104, 152, 4031$, $P = 0.018$. Each scavenger's distribution of different behaviours is visually demonstrated by percentage of total behaviour at feeding sites in Fig 2. With *a posteriori* Tukey HSD test, red fox shows significant difference in behaviour compared to badger ($p = 0.033$) and wolf ($p = 0.031$) but does not compared to marten or wild boar. Marten and wild boar shows no significant difference in behaviour to any of the other species. For estimating if the two most active scavengers, red fox and marten, differed in behaviour with other areas we tested vigilance against Swedish data, and no significant difference was found.
Vegetation coverage was high in 15.0%, medium in 40.5% and low in 44.5% of the camera sites. Wolves and badgers avoided open areas such as meadows and visited these areas in only 4.6% respectively 7.5% of their total visits. Avian scavengers and wolves preferred low vegetation and good visibility. Without snow coverage, red fox and wild boar appeared equally but when snow coverage at the site, red fox was the most active visitor. Avian scavengers seldom appeared when there was snow coverage and of mammals, nor did marten. No significant difference in feeding site selection related to visibility (Mann-Whitney: $U = 20$, $n = 7,7$, $P = 0.565$), snow coverage ($U = 15$, $n = 7,7$, $P = 0.224$) or vegetation coverage (Kruskal-Wallis: $H = 1.452$, $n = 7,7$, $P = 0.484$) in any of the scavengers. As seen in Tab 1, avian scavengers appeared most of all scavengers near human activity, whilst red fox was the most common mammal with 39.2% of all visits to feeding sites being <1 km from human disturbance. A Mann Whitey test shows no difference in feeding sites close to or further away from human activity between red fox, marten, badger and wolf (excluding wild boar): $U = 3$, $n = 4, 4$, $P = 0.149$. No difference between the two most visiting scavengers, red fox and marten either ($U = 1$, $n = 2, 2$, $P = 0.439$). A Kruskal-Wallis test shows significant difference in the 24 h scavenger activity pattern: $H = 10.37$, $n = 5,5,5,5,5$, $P = 0.016$. None of the scavengers showed any significant preference between full or new moon illumination (Mann-Whitney: $U = 12$, $n = 5, 5$, $P = 0.917$), nor was it shown when only comparing red fox and marten (Mann-Whitney: $U = 2$, $n = 2, 2$, $P = 1.0$).

Discussion

We will discuss the function and important factors regulating the level of vigilance in each of the four mammal scavengers; red fox, badger, marten and wolf since avian scavengers were very rare and wild boar did not use carcasses as an important source of food.

Red fox
Red fox were clearly the main scavenger with most visiting occasions during the three year study period. It showed the highest vigilance and apprehension, reflected in the behaviour of observing the camera most often of all the scavengers. Noticeable was

also the behaviour of looking upwards towards the tree canopy or sky, most often combined with a high level of vigilance, in spite of the very low density of avian predators in the Tuscan Apennines. Red fox are known to kill martens (Lindström et al 1995), but this behaviour appeared most often even when no martens had been observed before or after the red fox visit. Climbing trees only occurred in 0.4% of the marten visits in this study. Red fox followed all other scavengers, selected feeding sites in the forest with low vegetation coverage and good visibility, less snow and, of all mammalian scavengers, nearest human activity. They were mainly nocturnal but showed no attraction to crepuscular hours or lunar illumination even if somewhat more in full moon than new moon. The only predation risk demonstrated in this study for red foxes is from wolves which occurred much less at carcasses/feeding sites.

Aggregation with high numbers of subdominant species have been seen to defend or take over carcasses (Atwood and Gese 2008), but this was never observed in Alpe di Catenaia. Even if Italian wolves generally have a somewhat smaller body size than conspecifics in higher latitudes the size difference is still too decisive. Red fox and domestic dogs were never observed simultaneously or within short time intervals at the feeding sites, nevertheless, could be a potential risk as they occurred just as much as wolves but mainly during hunting seasons daytime. Moreover, several red fox individuals showed injuries such as limp and lost legs and eyes, which may indicate that they live under high predation pressure from solely wolf or both wolf and domestic dogs. In studies of sympatric canids the clear trend is for larger species to kill or displace smaller ones, resulting in habitat partitioning (Loveridge and Macdonald 2002). The higher red fox density shown by higher visits at feeding sites may explain that even if red fox avoid proximity to wolves, it is not enough to avoid the predation risk entirely, thereof, they have to trade-off other behaviours for vigilance.

Badger

Badgers has been classified as extreme specialist (Kruuk and Parish 1981) to generalist (Ciampalini and Lovari 1985) as well as adjustable to latitudinal variation (Goszczynski et al 2000). In Alpe di Catenaia, badgers did not feed on carcasses often, lacked vigilant behaviour as the only superior scavenger and possible predator is the wolf, but scent-market more than any other scavenger. They often scent-marked over other species markings which can be explained by that the territories are defended by occasional fighting and by a system of scent marking with latrines at their border (Roper et al 1993). Badgers followed red fox, which has been seen in previous studies (Macdonald 1987), and a few times also marten. Low vegetation coverage, good visibility, less snow and avoided human activity most of all scavengers. Mostly nocturnal and showed no attraction to crepuscular hours or lunar illumination. On the contrary, they visited more during new moon.

Pine and stone marten

Martens were the second most active scavenger which followed and is followed by red fox and badger. They arrived at feeding sites more rapidly than other scavengers after the previous visitor had left. They spend most time feeding and next after badger, the least vigilant, nonetheless, the smallest scavenging species. Moreover, they selected low vegetation with grass and shrub with poor visibility. Snow was avoided and moderately visiting sites near human activity. Entirely nocturnal and seem to prefer the darkness of new moon rather than full moon illumination. Contrasting to other studies where foraging is restricted and

adjusted due to predation pressure (Lima and Valone 1986), marten did not expressed a trade-off in foraging and anti-predator behaviour compared to other scavengers. They spent more time feeding than the others and, with the except of badgers, less time vigilant. This is the direct opposite of marten and red fox behaviour at carcasses in Sweden (Wikenros et al, unpublished), which suggests that marten has a latitudinal variation in anti-predator behaviour.

Grey wolf

Wolf was the fifth most active scavenger, however, domestic dogs which were slightly more active, are not natural scavengers and appeared very intensely during daytime primarily during the hunting season. Wolf followed only red fox and wild boar at a few occasions, and it is difficult to determine whether it was in search of carcasses in the case when after red fox, or after prey as wild boar is the main prey in Alpe di Catenaia (Davis et al. 2012). Wolves do kill red foxes that scavenge on their prey (Ståhlberg et al, unpublished), but the red fox may follow the wolf for abandoned kill leftovers (Jedrzejewski and Jedrzejewska 1992). Wolves scavenged moderately (11.2%) compared to the other scavengers in this study and to Swedish wolves (37.2%)(Ståhlberg, unpublished). They were next after red fox, the second most vigilant scavenger. They selected low vegetation with good visibility and avoided human activity. They were mainly nocturnal but also active during morning twilight until noon. As they were not GPS collared, they were not classified individually but judging by visual observations, the same individuals visited the same carcasses repeatedly.

Our second prediction that larger scavengers would follow smaller in a higher extent was partly supported by the study; the next largest scavenger, badger (7-17 kg) visited feeding sites <180 min after a previous scavenger had left in 12% of their total visits. Wolf which is the largest (31.7 kg),) followed others in 9.8%, marten (0.9-2.5%) followed others in 6.4% and red fox (5-7 kg) followed in 1.9%. However, marten was the quickest to arrive after other species with an average of 42 min, while red fox average was 77 min and badger 83 min, suggesting that marten are the optimal follower of other scavengers. Correspondingly with Swedish red fox and pine marten (Wikenros et al, unpublished), marten follows red fox within shorter time than vice versa.

Our last prediction that the low numbers of avian predators in the Tuscan Apennines would result in lower vigilance in scavengers was not supported by the study when comparing with south-central Sweden where ~4.5% of the scavengers are birds of prey (Ståhlberg, unpublished). When comparing vigilance behaviour, in Sweden and Italy (Wikenros et al, unpublished), red fox (19 and 23%), badger (0 and 1%) are rather similar, while marten (37 and 10%) and wolf (7 and 16%) differed vividly. Wolves show higher vigilance in Italy than in Sweden but as an apex predator, it has no relation to the predation risk in the scavenger guild.

Martens in Sweden show higher vigilance which may be explained by the predation risk of birds of prey. However, in Alpe di Catenaia, red fox (3%) and marten (0.7%) looked upwards towards the tree canopy or sky when visiting feeding sites although the lack of avian predators which was surprising. There are two characteristic features when classifying diurnal, nocturnal, crepuscular and moon illumination selection; martens selection of new moon with low moon illumination and wolf selection of morning twilight. Rasmussen and Macdonald (2011) suggested that light availability at night may influence activity patterns of wild dogs and cheetahs, and that nocturnal activity may be more pronounced than previously thought,

thus questioning the real role of lions and hyenas in influencing the activity patterns of subdominant species. The red fox shows somewhat higher selection of full moon than new moon and is most likely the highest predation risk factor for martens, why this may be a reason for martens choosing new moon rather than full moon illumination. Wolves visits at dawn (8.2%) were consistent with the activity peak shown by ungulates in the same area at that time and at dusk (Pagon et al 2013).

Conclusively, the lack of avian scavengers results in a clearly mammalian dominated scavenger guild in the wolf territory in Alpe di Catenaia. Even though wild boar is the most visiting species at the feeding sites, they barely scavenge which makes red fox the dominant scavenger followed by marten, badger, domestic dog and wolf. The ultimate follower was the marten with the shortest time until arrival after the previous visitor. Sites with low vegetation coverage with good visibility was selected by all scavengers except martens who selected poor visibility and low moon illumination. Feeding behaviour at carcasses was dominated by marten, vigilance (including looking upwards and at the camera) by red fox and scent-marking by badger. Many factors shape the interactions in scavenger guilds in wolf territories. At carcasses in Alpe di Catenaia, pine and stone marten balance the trade-off between feeding and vigilance in the most beneficial structure.

Acknowledgements
I am very grateful for the help I got from everyone who checked cameras and analysed films. The study was funded practical and financial by Arezzo Province, Axel and Margaret Ax:on Johnsons Foundation and Helge Ax:on Johnsons Foundation.

References

Atwood, T. C., and Gese, E.M. 2008. Coyotes (Canis latrans) and recolonizing wolves (Canis lupus): social rank mediates risk conditional behaviour at ungulate carcasses. Animal Behaviour, 75:753–762.

Berger, K.M., Gese, E.M., Berger, J. 2008. Indirect effects and traditional trophic cascades: a test involving wolves, coyotes, and pronghorn. Ecology, 89:818–828.

Beschta, R.L. and Ripple, W.J. 2009. Large predators and trophic cascades in terrestrial ecosystems of the western United States. Biological Conservation, 142:2401–2414.

Ciampalini, B. and Lovari, S. 1985. Food habits and trophic niche overlap of the badger *(Meles meles)* and the red fox *(Vulpes vulpes)* in a Mediterranean coastal area. Zeitschrift für Säugertierkunde, 50:226-234.

Durant, S.M. 1998. Competition refuges and coexistence: an example from Serengeti carnivores. Journal of Animal Ecology, 67:370-386.

Goszczynski, J., Jedrzejewska, B., Jedrzejewski, W. 2000. Diet composition of badgers (Meles meles) in a pristine forest and rural habitats of Poland compared to other European populations. Journal of Zoology (London), 250:495-505.

Griffin, A.S., Evans, C.S., Blumstein, D.T. 2002. Selective learning in a marsupial. Ethology, 108:1103-1114.

Harrington, L.A., Harrington, A.L., Yamaguchi, N., Thom, M.D., Ferreras, P., Windham, T.R., Macdonald, D.W. 2009. The impact of native competitors on an alien invasive: temporal niche shifts to avoid interspecific aggression? Ecology 90:1207–1216.

Hebblewhite, M., White, C.A., Nietvelt, C.G, McKenzie, J.A., Hurd, T.E., Fryxell, J.M., Bayley, S.E. and Paquet, P.C. 2005. Human activity mediates a trophic cascade caused by wolves. Ecology, 86:2135-2144.

Jedrzejewski, W., and Jedrzejewska, B. 1992. Foraging and diet of the red fox *Vulpes vulpes* in relation to variable food resources in Bialowieza National Park, Poland. Ecography, 15: 212–220.

Jennelle, C.S., Samuel, M.D., Nolden, C.A., Berkley, E.A. 2009. Deer Carcass Decomposition and Potential Scavenger Exposure to Chronic Wasting Disease. Journal of Wildlife Management, 73:655-662.

Kimbrell, T., Holt, R. D. and Lundberg, P. 2007. The influence of vigilance on intraguild predation. Journal of Theoretical Biology 249: 218–234.

Kittle, M.A., Fryxell, J.M., Desy, G.E., Hamr, J. 2008. The scale-dependent impact of wolf predation risk on resource selection by three sympatric ungulates. Oecologia, 157:163-175.

Kruuk, H. and Parish, T. 1981. Feeding specialization of the European badger *Meles meles* in Scotland. Journal of Animal Ecology, 50:773-788.

Lima, S. L. and Valone, T. J. 1986. Influence of predation risk on diet selection: A simple example in the grey squirrel. Animal Behaviour, 34, 536-544.

Lima, S.L. and Dill, L.M. 1990. Behavioural decisions made under the risk of predation: a review and prospectus. Canadian Journal of Zoology 68: 619–640.

Lindström, E. R., Brainerd S. M., Helldin, J. O. and Overskaug, K. 1995. Pine marten - red fox interactions: a case of intraguild predation? Annales Zoologici Fennici, 32, 123-130.

Linnell, D.C. And Strand, O. 2000. Interference interactions, co-existence and conservation of mammalian carnivores. Diversity and Distributions, 6:169–176.

Loveridge, A. J. and Macdonald, D. W. 2002 habitat ecology of two sympatric species of jackals in Zimbabwe. Journal of Mammalogy, 83:599-607.

MacArthur R.H., Pianka E.R. 1966. On optimal use of a patchy environment. American Naturalist, 100:603-609.

Macdonald, D. W. 1987. Running with the fox. London: Unwin Hyman, UK.

Macdonald, D. W., Buesching, C. D., Stopka, P., Henderson, J., Ellwood, S. A., Baker, S. E. 2004. Encounters between two sympatric carnivores: red foxes *(Vulpes vulpes)* and European badgers *(Meles meles)*. Journal of Zoology, 263:385–392.

May, R., van Dijk, J., Wabakken, P., Swenson, J.E., Linnell, J.D.C., Zimmermann, B., Odden, J., Pedersen, H.C., Andersen, R., Landa, A. 2008. Habitat differentiation within the large-carnivore community of Norway's multiple-use landscapes. Journal of Applied Ecology, 45:1382–1391.

Merkle, J.A., Stahler, D.R., Smith, D.W. 2009. Interference competition between gray wolves and coyotes in Yellowstone National Park. Canadian Journal of Zoology, 87:56-63.

Pianka E. R. 1974. Niche Overlap and Diffuse Competition. Proceedings of the National Academy of Sciences of the United States of America 71: 2141–2145.

Quenette, P.Y., 1990. Functions of vigilance behaviour in mammals: a review. Acta Oecologica 11, 801–818.

Rasmussen, G. S. A., and D. W. Macdonald. 2011. Masking the zeitgeber: African wild dogs mitigate persecution by balancing time. Journal of Zoology 286:232–242.

Roper, T.J. & Lüps, P. 1993. Disruption of territorial behavior in badgers *Meles meles*. Zeitschrift für Säugetierkunde, 58:252–255.

Schoener, T.W. 1974a. Resource partitioning in ecological communities. Science, 185:27-39.

Sih, A. 1980. Optimal behavior: Can foragers balance two conflicting demands? Science, 210:1041-1043.

Sönnichsen, L., Bokje 2013 M., Marchal, J., Hofer, H., Jedrzejewska, B., Kramer-Schadt, S., Ortmann, S. 2013. Behavioural responses of European roe deer to temporal variation in predation risk. Ethology, 119:233-243.

Tinbergen, J.M. 1981. Foraging decisions in Starlings *(Sturnus vulgaris L.)*. Andrea, 69:1-67.

CONCLUSIONS

In this thesis, causes by ecological factors and consequences in different latitudes have been investigated. As shown, predator-prey constitutions are formed by habitat heterogeneity which is greatly influenced by human landscape use and activity. Prey density is often used for predicting predator feeding ecology, not always taking into account predator and prey behaviour. Latitudinal variances are also reflected in both predator and prey behaviour. Prey selectivity was relative rather than absolute. The results in this thesis support the argument of flexibility and adaptability in grey wolf in highly diverse habitat conditions. Also anti-predator behaviour is a very elastic mechanism in scavengers feeding under predation-pressure.

ACKNOWLEDGEMENTS

I will begin by thanking **Anders Angerbjörn** who, many years ago, explained exactly how one should accomplish the Master degree as the Bologna process was to change the qualification requirements for future possibilities. I did as he suggested, otherwise I would not have been here today.

Luckily, I met **Marco Apollonio** at a conference in Berlin and he gave me the opportunity to apply for the PhD programme in Italy. We have not always understood each other – but I am very over that I have done my PhD programme in Italy! I have studied and worked in several countries, but Italy has been a challenge for me – both as a female in the society and as a student in the scientific world! I've learnt a lot these years and I want to say GRAZIE MILLE to **Marco, Elena Bassi, Andrea Marcon, Emanuela Donaggio, Daniele Battocchio** and **Stefania Boschettos** who I worked with – you were all absolutely great! Also, I am very thankful for data and hard work done by **Sabrina Müller** and all people in Scandinavia collecting and anaylising data.

None of this would have been financially possible if it was'nt for **Axel and Margaret Ax:on Johnsons Foundation** and **Helge Ax:on Johnsons Foundation**.I will continue in Swedish now… Ni var helt fantastiska som gav mig möjligheten att göra det många svenskar anser är omöjligt – jag och mina söner har klarat oss sedan 2010, TUSEN TACK till Er!

Den som ledde in mig på vargens spår var **Håkan Sand** och hans team! Jag har alltid beundrat rovdjuren och varit oerhört intresserad av dem men hade det inte varit för dina "extra utflykter" till reviren för märkning och valpkoll så hade jag kanske aldrig blivit så frälst vid tanken att faktiskt kunna arbeta med dem i framtiden! TUSEN TACK till dig med! På vägen fick jag även hjälp av **Birgitta Tullberg** vilket jag hjärtligt uppskattade! Jag är ju inte klar med publiceringarna än men där har jag **Camilla Wikenros** som säkert har en hel del mer att träna upp mig inom – TUSEN TACK så här långt!

Sist men absolut inte minst – de som stöttat mig mest och fått utstå barn/hundpassning, flytt till pizzaland med ny kultur och skola med nytt språk – **mamma, pappa, Oscar och Gustav!** Ni har varit helt FANTASTISKA och jag är skyldig er alla mycket mer än ord kan beskriva, puss och kram!

"Our greatest glory is not in never falling, but in rising every time we fall."
Confucius